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AN INVESTIGATION OF PHOTOSYNTHETIC C-FIXATION IN FYNBOS GROWTH FORMS AND ITS VARIATION WITH SEASON AND ENVIRONMENTAL CONDITIONS

By

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A thesis presented for the degree of

Master of Science

at the University of Cape Town

March 1988

ABSTRACT

The seasonal and diurnal patterns of photosynthetic gas exchange and the water relations of seven species of the mediterranean-climate region of South Africa (fynbos) were investigated. The following species, representing the major fynbos elements, were chosen for intensive investigation: Erica plukenetii and Erica hispidula (ericoid element), Thamnochortus lucens and Askidiosperma paniculatum (restioid element), Protea laurifolia and Leucadendron salignum (proteoid element). Metrosideros angustifolia, a shrub of riparian habitats, was also studied.

The restioids and the ericoids experienced the lowest photosynthetic capacities of all the species studied. In general, a decline in net photosynthetic rates was observed during summer. However, a resprouter proteoid, L.salignum, reached its maximum photosynthetic capacity during summer. The degree of summer decline in net photosynthetic rate was more pronounced for the shallow-rooted ericoids restioids than for the proteoid species and the shrub of riparian habitats. Photosynthetic capacity generally decreased with increasing plant water stress. Because the shallow-rooted species experienced their lowest tissue water status during summer, at a time when their lowest photosynthetic capacities were recorded, it was concluded that photosynthetic capacities were deterimined

to some extent by degree of plant water stress. Since the summer decline in photosynthetic capacity was not always paralleled by depressions in stomatal conductance or tissue water status, it was reasoned that water shortage during summer could not have been the only and most important factor causing the decline in photosynthetic capacity. To determine the possible contribution of high temperatures to the summer decline in photosynthetic capacity, the photosynthetic temperature responses of species representative of restioid, ericoid and proteoid elements were investigated. During summer, net photosynthetic rates declined at temperatures above 20^{o}C which indicate that the depressed photosynthetic capacities measured during summer could also be attributed to the effects of high temperature.

The photosynthetic responses to single environmental factors (temperature and irradiance) were not similar for all the species studied. Light saturation of an ericoid species, E.plukenetii, was recorded at significantly lower photon flux densities than for a proteoid species and a restioid species. The restioid species studied, T.lucens, changed its photosynthetic temperature optimum from spring to autumn while the ericoid and proteoid species maintained apparently constant photosynthetic temperature optima during these seasons. The unique photosynthetic irradiance response of the ericoid species

studied and the ability of the restioid species to change its photosynthetic temperature optimum possibly have some role to play in the distribution patterns of these species.

The efficiency of water usage with respect to carbon gain of the various species was investigated. Those plants which maintained relatively high photosynthetic capacities throughout the year (proteoids) and those which were able to control excessive water loss (ericoids) were more efficient in utilizing water as a resource. The restioid species lost the most water in relation to carbon gained. The inferior water use efficiency of this species, particularly during summer, appears to be counterbalanced by an ability to respond quickly to short irregular periods of rain. The restioid species responded with increased photosynthetic rates and stomatal conductances when irrigated during summer. However, there were no appreciable differences between the photosynthetic rates of the control and irrigated individuals of the proteoid and ericoid species.

Monthly carbon gain was estimated by taking seasonal variation in daylength and the seasonal variation in cloud cover into consideration. It would appear that the proteoid species fixed most of their carbon during summer, and the restioid and ericoid species during spring. In comparing the measured periodicity of plant vegetative growth and the seasonal variation in carbon

gain it appears that the fynbos species invest a major portion of the most recently produced photosynthates during the most productive part of the year to growth and development. If carbon gaining capacity can be considered as potential competitive ability, then the data obtained provide some support for a recent post-fire regeneration model . The regeneration model demonstrated that the proteoid element (high carbon gain) contributes an increasingly greater percentage to the plant population at a time when the proportional representation of the ericoid and restioid elements (low carbon gain) decline. The lower carbon gaining capacities of the ericoid and restioid species could therefore be interpreted as contributing to their poor competitive ability during the later succesional stages when competition for resources increases.

ACKNOWLEDGEMENTS

I would like to express my appreciation to the following institutions and persons for their support and guidance.

* My supervisor, Prof.O.A.M. Lewis, for unfailing support, guidance and encouragement. The advice and constructive criticisms concerning the production of this manuscript are particularly appreciated.

* The CSIR, Foundation for Research Development, Fynbos Biome Project, for financial support which made this project possible.

* The staff at the Botany Department, University of Cape Town for support and encouragement.

* The South African Forestry Department for permission to carry out field experiments in the Bain's Kloof Forestry Reserve. Mr. Grobler and Mr. Wilmans who gave me access to their weather data.

* Finally, I would like to thank my parents for the encouragement and support that they have provided through the years.

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CHAPTER 1: INTRODUCTION

The fynbos biome is one of five mediterranean-climate regions of the world. It is characterized by dry summers and wet to mild winters (Aschmann, 1973). It is also noted for being nutrient-poor (Kruger et al., 1983). Early studies undertaken by researchers in the fynbos biome were aimed at defining geographical distribution, extent of major vegetation types and the provision of data describing community structure and function and the related physical environmental variables (Boucher & Moll, 1980; Kruger, 1977; Kruger & Taylor, 1979). This approach, with the wealth of resulting detail, has led to the development of a corpus of fynbos ecological knowledge. In order to obtain a greater understanding of the observed ecological phenomena, further study in the direction of analyzing plant processes is necessary. Process physiology provides an insight into the strategies employed by plants to adapt to environmental conditions.

Of all the various plant sub-systems which define physiological adaptation, processes associated with plant growth and development are probably the most important. Because of the central nature of plant productivity to all aspects of growth and development it could be regarded as a subject that warrants initial investigation in any attempt to understand how processes relate to ecological phenomena. Plant productivity is a

function of photosynthesis and respiration (dark and photorespiration). This investigation, however, was essentially concerned with understanding the manner in which carbon fixation is integrated with the environment to produce the response shown by plants in their natural environment. Respiratory loss of carbon from plant parts was not addressed by this investigation. One of the objectives of this investigation was to determine the net photosynthetic rate (gross photosynthetis - photorespiration) of the different fynbos elements and its variation with season, environmental variables and phenological stages.

Since both daytime carbon gain and water loss by transpiration are controlled by stomatal conductivity and because of seasonal limitations on water supply in the biome, emphasis was also placed on water as a factor determining carbon fixation rates. Furthermore, a knowledge of CO_2 uptake and water loss will allow a direct assessment of the water-use-efficiency.

To quantitatively assess the importance of single environmental factors on plant production, photosynthetic studies were carried out under a range of irradiances and temperatures. Correlations were also sought between phenology and photosynthetic capacity. Admittedly, such an approach could be considered as being superficial since allocation pattern of fixed carbon explains seasonal phenological phenomena more accurately than maximum carbon fixation rates at a particular time. It was hoped,

however, that the treatment adopted in this study would be able to fill some of the gaps in the present understanding of fynbos function.

This investigation has concentrated on the following aspects of photosynthetic C-fixation which were considered to be important in setting out to describe functioning of fynbos ecosystems.

a) To determine the photosynthetic C-fixing capacity of the different fynbos elements.

b) To determine the seasonal changes in photosynthetic capacity and related gas exchange processes (transpiration rate and stomatal conductance).

c) To determine the diurnal rythms of photosynthetic capacity and related gas exchange processes during the different months of the year.

d) To find out how photosynthetic capacity correlates with plant water status.

e) To determine the response of photosynthetic gas exchange processes to addition of water (irrigation).

f) To establish the relation between photosynthetic rate and changes in temperature and irradiance.

g) To determine the efficiency of water usage (with respect to carbon gain) of the various growth forms.

h) To determine how photosynthetic capacity correlates with vegetative growth phases.

Before embarking on a full-scale monthly program of field investigation, preliminary studies were undertaken to establish the degree of variation in photosynthetic gas exchange processes with leaf age, orientation and position on plant. This enabled clear definitions of the nature which measurements were going to take. The results of these studies are dicussed in section 3.7.

CHAPTER 2

A LITERATURE REVIEW OF RELEVANT PHOTOSYNTHESIS STUDIES

2.1 General

To establish correlations between plant photosynthetic responses and environmental conditions, and to interpret this behaviour at the physiological or ecological level, two approaches have been adopted by workers in this field. Firstly, net photosynthesis has been investigated in relation to the naturally occurring environmental conditions in the field. Secondly, the importance of single environmental factors have been determined by carrying out experiments under artificially changed conditions in the laboratory and in the field.

To isolate the environmental determinants of photosynthetic capacity, most workers have recorded appropriate environmental factors in addition to carbon dioxide exchange rates. Such variables include temperature, light intensity, soil water content, air humidity and ambient air carbon dioxide concentrations prevalent at the time of observation. A number of studies have also focused on photosynthetic rate in relation to physiological factors. Strain (1969), for example, investigated possible relationships between photosynthetic

capacity and seasonal patterns of carbon allocation.

Much of the observed seasonal and diurnal photosynthetic variability in many plant species have been assessed in relation to levels of plant or soil water status. In such studies factors such as water content, water potential, soil water potential, stomatal conductivity and transpiration rate were usually investigated in addition to rates of photosynthetic gas exchange. Numerous examples of studies of this kind are reviewed in sections 2.2 and 2.4.

Measurements of gas exchange by different leaf age classes have revealed declining photosynthetic rates with increasing leaf age (Freeland, 1952, for conifers; Hardwick et al., 1968, for Perilla; Syvertsen & Cunningham, 1977, for Larrea sp.). From studies on seasonal carbon dioxide exchange in pine seedlings, Drew and Ledig (1981) reported high gas exchange rates in primary needles which declined at the time of secondary needle emergence. Reader (1978) (for Erica sp.) and Hom & Oechel (1983) (for Picea) have observed higher photosynthetic rates in young chlorophyllous tissue as opposed to older tissue of these species.

Fertilization and irrigation studies have been carried out to determine the effects of these practices on the photosynthetic rates of plants native to nutrient-poor or water stressed environments. NPK fertilizations were found to depress

photosynthetic rates in vascular arctic species (Bigger & Oechel, 1982). Decreased photosynthetic rates were also observed following increased nitrate supply to an evergreen chaparral species by (Oechel et al. 1981b). These photosynthetic responses following nutrient additions cannot easily be explained in terms of the nutrient controls of photosynthesis. Irrigated evergreen scleromorphic shrubs had higher photosynthetic rates than the unirrigated ones during summer (Gigon, 1979).

2.2 Studies in Mediterranean Ecosystems

There has been considerable recent interest in the assessment of ecophysiological behaviour of plants native to mediterranean climates. These studies provide physiological bases for an understanding of ecological relationships. Investigations of this nature also provide a conceptual framework to explain the ability to adapt to unique environmental factors (Miller, 1981; Margaris & Mooney, 1981; Kruger et al., 1983).

Several stresses are imposed on plants native to mediterranean regions as a result of the characteristic environmental conditions. Mediterranean climates have moderate rainfall and cool temperatures in winter followed by hot, dry summers (Aschmann, 1973). Another unifying aspect of mediterranean region ecology is their occurrence on nutrient poor soils (Kruger et al., 1983). The long summer drought in particular

should place severe constraints on the growth and development potential of the resident plants.

Photosynthetic studies confirm great differences in the carbon gaining potential of the different plant elements of the mediterranean regions of California and Chile (Mooney & Dunn, 1970; Harrison et al., 1971; Mooney et al., 1975; Gigon, 1979; Oechel & Mustapha, 1982). These authors have noted a strong correlation between rates of daily carbon uptake and numerous environmental factors. Less extensive photosynthetic studies have been undertaken in mediterranean-climate Australia (Hellmuth, 1971) and in mediterranean proper (Margaris, 1977).

A number of studies on plants of central Chile and southern California indicated intrinsic differences in the photosynthetic capacities of life-forms native to these regions. The observed variability in photosynthetic capacity was considered to reflect adaptive carbon-gaining strategies, in which the predominance of each strategy corresponds to a position on a gradient of environmental stress. Degree of water stress, for example, has been used in most studies to explain the observed differences in carbon-gaining capacities (Mooney & Dunn, 1970; Harrison et al., 1971; Mooney et al., 1975; Gigon, 1979, Oechel & Mustapha, 1982). In addition, morphological and physiological attributes were identified as supportive evidence for hypotheses relating carbon-gaining capacities to the intensity of moisture stress (Oechel et al., 1981a).

Harrison et al. (1971) compared the photosynthetic drought relationships of evergreen chaparral and drought-deciduous coastal sage species. Both plant communities occur in mediterranean-climate California and are subject to summer drought. The coastal sage habit, however, is more xeric. The coastal sage species with high gas-exchange rates appear to be highly sensitive to drought stress and unable to control their transpirational water loss. Lower photosynthetic and transpiration rates were observed in the evergreen chaparral species. Harrison et al. (1971) suggested that the sclerophyllous nature of the leaves and the deeper and more extensive rooting systems of the evergreens aided their year round carbon-gaining capacity. An analysis of the environmental limitations on the photosynthetic capacity of a California evergreen sclerophyll (Mooney et al., 1975) has also shown that water availability is the primary seasonal limitation of carbon gain followed by photoperiod and, to a lesser extent, temperature.

Numerous studies have reported a higher inherent photosynthetic capacity on a unit-leaf-area basis for drought-deciduous species as opposed to evergreen species (Harrison et al., 1971; Mooney & Dunn, 1970; Gigon, 1979; Oechel & Mustapha, 1979; Oechel et al., 1981a). Although drought deciduous species bear leaves only for a limited period, their high photosynthetic rates allow them to equal the carbon gain of the evergreen sclerophylls (Mooney & Dunn, 1970). Heteromeles arbutifolia, a California

evergreen shrub, photosynthesized throughout the year, but daily carbon gain varied considerably (Mooney et al., 1975). Summer depressions in photosynthetic rate were due to summer drought and the short photo-period was suggested as being the causal factor for reductions in carbon gain during winter. The summer drought limitation of carbon gain in evergreens was illustrated by Gigon (1979) who observed considerably higher photosynthetic rates in certain irrigated shrubs as opposed to unirrigated shrubs.

An intensive investigation of the similarities in physiological processes and in resource-use efficiency associated with carbon uptake between plants of mediterranean Chile (matorral) and California (chaparral) was undertaken by Oechel et al.(1981a). Species were chosen in paired samples with identifiable growth patterns in both regions. Consideration was given to cover-abundance, morphology, habitat and physiology in choosing the species to form pairs. Chilean species showed significant and consistently higher maximum photosynthetic rates than did their paired California counterparts. In California, the maximum carbon uptake rates on a leaf-area basis decreased as follows: drought deciduous shrubs, perrenial herbs (geophytes), annual herbs (annuals), evergreen sclerophyllous shrubs and succulents. Chilean species showed relationships between growth form and carbon uptake rate similar to that of the chaparral species. The overall pattern of photosynthetic carbon uptake rates by growth form was: drought deciduous annual herbs,

perrenial herbs, photosynthetic stem shrubs, evergreen sclerophyllous shrubs and succulents (Oechel et al., 1981a).

Oechel & Mustapha (1982) conducted a study of the geographic variability in photosynthesis along an elevational transect from inland to coastal California. These authors used incorporation of Carbon-14 as a measure of photosynthesis. Photosynthetic rates were found to be closely related to level of water stress which in turn was found to be asociated with annual precipitation (geographical variation) and rooting depth.

A strong pattern emerged from an investigation of the extent of correlation between percent cover in chaparral evergreen shrubs (success of plant species) and rate of carbon assimilation (Oechel & Mustapha, 1979). Photosynthetically active species were more abundant at each elevation.

Mooney & Chu (1974) investigated the efficiency with which carbon was fixed into dry matter, and to the adaptive value of possible seasonal changes in carbon allocation in chaparral species. The authors found that more carbon was allocated to storage and structure during periods of low water availability than to metabolism.

There is a paucity of information available regarding correlations between nutrient limitations or additions and photosynthesis in Mediterranean ecosystems. Even the effects of

fertilization on photosynthetic rates in agricultural species remain unclear. The dramatic increase in photosynthetic rate of Adenostoma fasciculatum burn resprouts, however, was thought to have resulted from nutrient enhancement following fire since resprouts from hand-cleared areas did not exhibit the same elevated photosynthetic rates (Oechel & Hastings, 1983).

Oechel et al.(1981b) explored the extent of nitrogen as a limiting factor of photosynthesis. Gas-exchange measurements were performed on Ceanthus crassifolius fed with different levels of nitrate. Nutrient treatments consisted of 1, 2, 10, 15 and 20 mM nitrate levels with all other nutrient elements at the same concentrations. Increased growth rates occurred with elevated nitrogen levels. Surprisingly, reduction in photosynthetic rate on a leaf area basis was experienced with increased nitrogen levels. Depressed respiration rates were observed at elevated nitrogen treatments. The authors suggested that addition of a single element, such as nitrogen, created new nutrient stresses within the plant. A balanced nutrition appears to be a prerequisite for elevated photosynthetic rates.

Very little attention has been given to studies on photosynthetic enzyme content. Such studies could elucidate the controls of photosynthetic activity provided correlations are found between levels of seasonal enzymatic activity and environmental variables such as light, temperature, nutrients and water status.

2.3 Photosynthetic Studies in Arctic and Alpine Ecosystems.

Various authors have investigated the rates of photosynthesis of plants experiencing extremely low seasonal temperatures (Smith & Hadley, 1974; Vowinckel et al., 1975; Lawrence & Oechel, 1983; Hom & Oechel, 1983). Their work has revealed different degrees of plant photosynthetic and physiological adaptation of the native plants to the harsh climatic regime of these areas. These studies also reflect the overriding effects of temperature and light intensity on photosynthetic capacity of plants native to these colder regions. The existence of temperature-related photosynthetic and respiratory acclimatization responses, for example, has been demonstrated for alpine and subarctic populations of Ledum groenlandicum, an ericaceous shrub species (Smith and Hadley, 1974).

Vowinckel et al., (1975) investigated the diurnal and seasonal variation of photosynthesis of Picea mariana in the Canadian subarctic region. The relatively high light saturation level for photosynthesis reflects the possible limitation of light intensity on diurnal photosynthetic rates during summer. The photosynthetic temperature optimum was recorded between 13^{o}C and 15^{o}C, and 30% of the maximum rates occurred at 0^{o}C. This study by Vowinckel et al., (1975) clearly illustrated photosynthetic adaptation to the existing climatic regime.

The effect of laboratory soil-temperature treatment on photosynthetic characteristics of four common Alaskan hardwoods was investigated by Lawrence & Oechel (1983). Maximum photosynthetic rates in the order of 9,5 $mgCO_2$ dm^{-2} h^{-1} were observed at higher temperatures (25°C soil and air temperature). The authors suggested that the effects of cold soils on water transport in roots could be the principal cause of the observed reductions in photosynthesis and conductance.

2.4 Photosynthetic Studies in Desert Ecosystems.

Limited supplies of water and very high air temperatures prevalent in summer in many of the world's desert regions impose special demands on plants occupying such habitats. Survival in these extreme habitats involves not only efficient photosynthetic water use but also the capacity to acquire and transport water under great evaporative demands. Numerous studies have shown that desert shrubs possess special morphological and physiological characteristics to maximize photosynthesis within the constraints of their available resources and physical environment (Strain, 1969; Oechel et al., 1972; Odening & Strain, 1974; Bjorkman et al., 1972; Schulze et al., 1975; Solbrig & Orians, 1977).

Bjorkman et al., (1972) investigated the photosynthetic performance of Tidestromia oblongifolia, a low-growing herbaceous perennial native to Death Valley, California. In contrast to observations for Picea mariana in the subarctic (Vowinckel et al., 1975) the photosynthetic rate for T.oblongifolia was a linear function of light intensity up to the highest light intensity received by the plant. At the highest level of irradiance the maximum photosynthetic rate (20 μMol dm^{-2} min^{-1}) was reached at about 47°C.

The literature suggests that observed photosynthetic rates are largely governed by moisture stress and secondarily by temperature. Odening & Strain (1974) suggested that desert species could have adapted to desert conditions in diverse ways which allowed them to maintain a positive carbon balance for a maximum period. These adaptations appear to be related to patterns of water-use efficiency (e.g. deciduous vs evergreen habit). Similarly, Oechel et al., (1972) considered tissue water potential as the most important factor controlling photosynthetic capacity of Larrea divaricata, an evergreen xerophytic desert shrub. In contrast, drought deciduous desert shrubs experienced large seasonal fluctuations in photosynthetic rate as well as more pronounced seasonal changes in total carbohydrate reserves than Larrea (Strain, 1969). These observations indicate that photosynthetic patterns in desert

shrubs are largely determined by degrees of physiological adaptation which allow metabolic activities at low water potentials.

CHAPTER 3

MATERIALS AND METHODS

3.1 STUDY AREA AND SPECIES STUDIED

The study site (alt. ca 730 m) was located in the Bain's Kloof Forestry Reserve ($33^{o}\ 34^{1}S$: $19^{o}06^{1}E$) outside Wellington, in the Slanghoek mountain range of the Cape Province, South Africa (fig.3.1). The plant communities at the study site occurred on soils derived from sandstone and quartzites of the Cape Folded Belt. The soil phosphorous composition at Bain's Kloof was investigated by Witkowski & Mitchell (1987). The climate of the region is a true Mediterranean climate with dry summers and wet winters (Schulze, 1947).

Unfortunately, collection of meteorological data at the closest weather station (Tweedetol) was terminated during the initial stages of the study period. To obtain some indication of the seasonal variation in ambient temperature and precipitation,

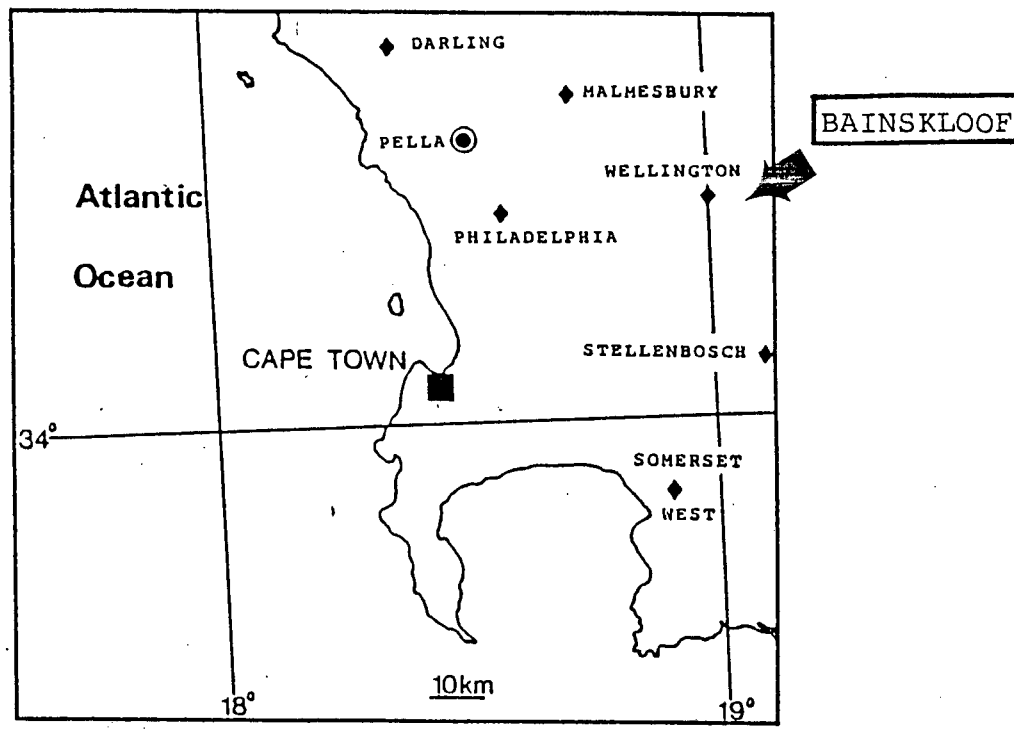


Figure 3.1: Location of the Bain's Kloof study site in the South Western Cape, South Africa.

unpublished records from the Hawequas weather station (33° 44¹S : 19°04¹E) of the South African Forestry Department were used. The variation in mean daily midday temperatures for the various months at Hawequas from April 1983 to April 1986 is shown in fig.3.2. The mean monthly rainfall (fig.3.3) and the mean number of days with rain (fig.3.4) were also calculated using the Hawequas rainfall records from 1976 to 1985. The vegetation of the study area was approximately four years old, having regenerated after a fire in 1981. Moll et al.(1984) have reclassified the vegetation units of the fynbos biome and on the basis of their classification system the Bain's Kloof study site was considered as consisting of Wet Mountain Fynbos communities. In the mature stage, the vegetation is dominated by members of the Proteaceae with Protea laurifolia and Leucadendron salignum being prominent shrubs.

Species were selected to be representative of the three characteristic fynbos elements: the proteoid, ericoid and restioid elements (Taylor, 1978). Two dominant species of each growth form were selected for intensive investigation.

Ericoid growth form:

Erica plukenetii L. (Figure 3.5)

Erica hispidula L. (Figure 3.6)

Restioid growth form:

Thamnochortus lucens Pill (Figure 3.7)

Askidiosperma paniculatum (Masters) Linder (Figure 3.8)

Proteoid growth form:

Protea laurifolia Thunb. (Figure 3.9)

Leucadendron salignum Bergius (Figure 3.10)

To analyze differences in photosynthetic gas exchange processes in relation to plant age, measurements were also performed on mature individuals of Protea laurifolia (Figure 3.11) which were approximately 30 years old at the time of measurement. These individuals were growing on a site which was unaffected by the fire.

Measurements were also performed on Metrosideros angustifolia (L.) Smith (figure 3.12), a shrub of riparian habitats. Since the proteoid species were growing on a well drained soil, M.angustifolia was selected for intensive investigation to allow comparison of photosynthetic behaviour of shrubs of similar growth form but in contrasting habitats.

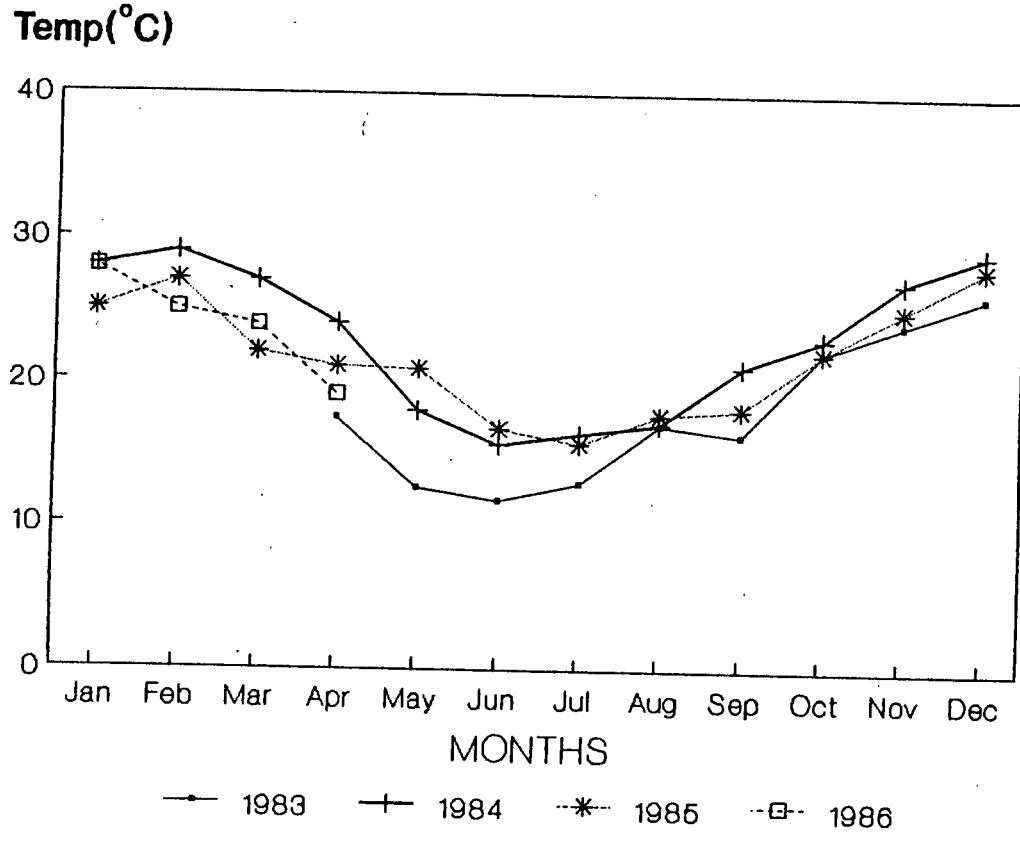


Fig.3.2: The mean monthly midday temperatures measured at Hawequas weather station from April 1983 to April 1986.

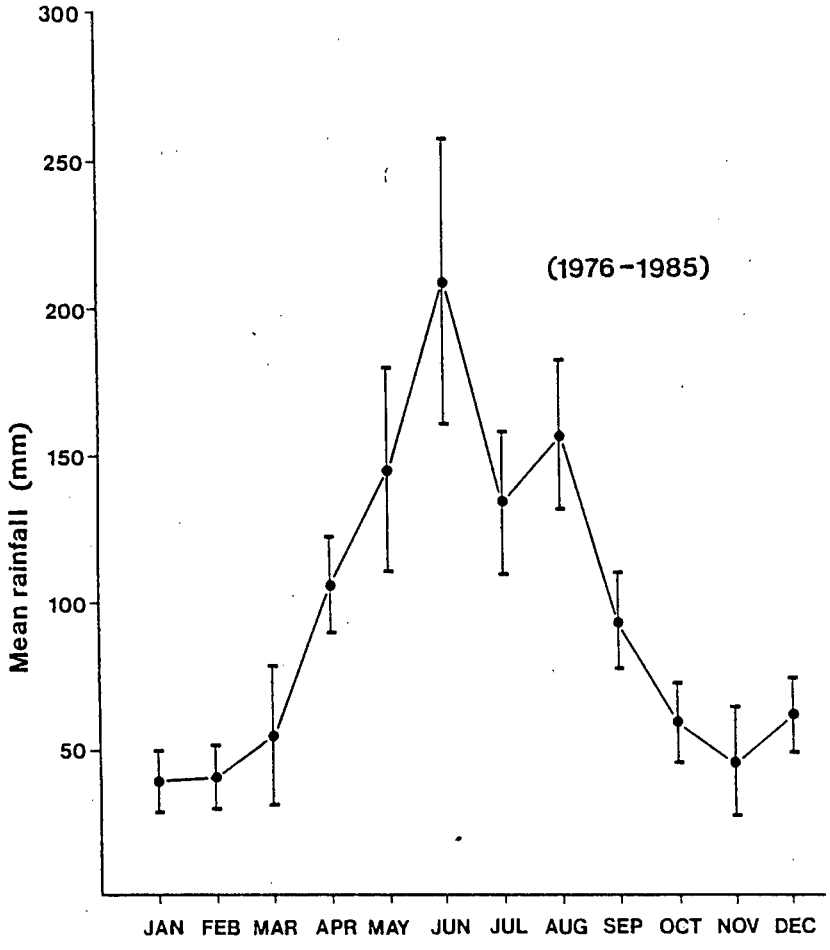


Fig.3.3: The mean monthly rainfall measured at Hawequas weather station from January 1976 to December 1985.

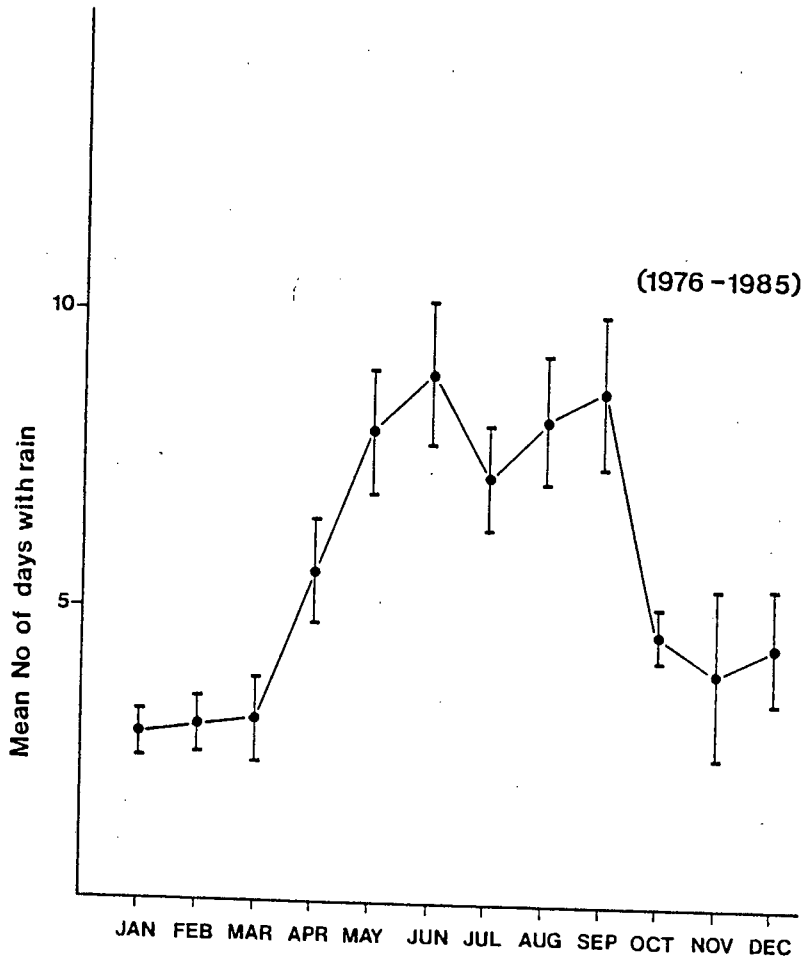


Fig.3.4: The mean monthly number of days with rain measured at Hawequas weather station from January 1976 to December 1985.

Fig.3.5: A three to four year old individual of Erica plukenetii L.

Fig.3.6: A three to four year old individual of Erica hispidula L.

Fig.3.7: A three to four year old individual of Thamnochortus lucens Pill

Fig.3.8: A three to four year old individual of *Askidiosperma paniculatum* (Masters) Linder

Fig.3.9: A three to four year old individual of *Protea laurifolia* Thunb.

Fig.3.10: Three to four year old individuals of *Leucadendron salignum* Bergius

Fig.3.11: A ca 30 year old individual of *Protea laurifolia* Thunb.

Fig.3.12: Four to five year old individuals of *Metrosideros angustifolia* L.

3.2 MEASUREMENT OF XYLEM PRESSURE POTENTIAL

To understand the plant photosynthetic response to decreasing levels of available moisture it was necessary to obtain some measurement of internal plant water status. A relatively large number of methods for the determination of plant water status have been described (Slavic, 1974). The pressure bomb technique (Scholander et al., 1965) for measuring water potential was used during this study because of its simplicity and because the instrumentation is well adapted for operation in the field . Moreover, this technique has been used quite extensively for fynbos water relations studies (Jeffery et al., 1987; Miller, 1985; Miller et al., 1984; Miller et al., 1983; Sommerville, 1983).

The water potential in a plant cell is usually negative as it is less than that of pure water. The four components of water potential are: osmotic, pressure, matric and gravitational. Altidudinal displacement of water from a reference height results in small changes in gravitational potential (Boyer,1969). The gravitational component of water potential was considered negligible in this study because all measurements were performed on plants of comparable height. Since the

osmotic and matric components are considered constant or negligible (Boyer, 1969), pressure potential measurements, recorded with a pressure bomb, were assumed to closely approximate the plant water potential.

Water potential measurements were performed before dawn and around midday (11h00 - 13h00). Pre-dawn was considered as the period prior to increases in temperature or light intensity at the start of the day. A pressure bomb with a 40 bar pressure limit was used (PMS Instrument Co., Corvalis, USA).

The excised plant part was put in the pressure chamber with the cut end in view. The pressure was then applied and water potential recorded as the pressure at which the cut end slickens. The rate of increase in air pressure was kept constant and the interval between cutting and measurement was kept to a minimum (Ritchie & Hinckley, 1975).

Vegetative shoots of the ericoid species and of Metrosideros angustifolia and Leucadendron salignum were used for the measurement of water potential. Flowering culms of the restioids and individual leaves of the juvenile and mature individuals of Protea laurifolia were used for these measurements.

Intraspecific variation was kept to a minimum by selecting

individuals of similar size, age and height (Waring and Cleary, 1967). In addition, exposure to the sun presented an appreciable source of variation. Since one of the primary interests in this study was the relationship between maximum C-fixation and plant water status, sun exposed plant material was chosen for water potential measurements throughout the study.

3.3 MEASUREMENT OF RATES OF PHOTOSYNTHETIC GAS EXCHANGE

Gas exchange by photosynthetic organs of fynbos species was measured by using infra-red gas analysis. This technique is based on the ability of heteroatomic molecules to absorb specific wavelengths of infra-red radiation (IR) with each molecular species having a characteristic absorption spectrum. With this system, air to be analysed for the concentration of a particular heteroatomic gas is passed through an analysis tube of an infra-red gas analyser (IRGA). Infra-red radiation is then shone through the analysis tube and the reduction in IR radiation is indicative of the concentration of a particular heteroatomic gas (Long, 1982). To measure respiratory or photosynthetic CO_2 exchange, for example, a leaf is enclosed in a chamber through which air is passed. The incoming and outgoing airstreams are then analysed by an IRGA for the comparison of CO_2 concentrations. Transpiration rate can be calculated from measured air flow rates and water vapour concentration differences between air entering and that leaving a chamber (Janac et al.,1971). Stomatal conductances can also be determined from the measured relative humidity, temperature, and volume flow rate (Parkinson et al., 1980).

A transportable system for field measurement of plant gas

exchange was employed for this study. It consisted of an IRGA (LCA-2, Analytical Development Company Ltd., Hoddesdon, England) which was used as an open system in the differential mode. This system enabled the continuous correction of measurements for changes in IR source and IR detector characteristics (eg. changes due to temperature). The Parkinson Leaf Chamber (PLC, Analytical Development Company Ltd., Hoddesdon, England) was used in conjunction with the IRGA. The leaf was sealed into the chamber by neoprene rubber gaskets. The chamber contained a humidity sensor, photocell, thermistor, and a fan which was positioned to allow efficient gas-mixing and rapid thermal equilibrium. Ambient air was supplied at constant rate by an air supply unit with a variable area flow meter (ASU, Analytical Development Company Ltd., Hoddesdon, England). The rate of air delivery was maintained at 200 ml min^{-1} for all measurements. The ASU was fitted with drying columns to supply dry air to the chamber. Magnesium perchlorate was used as a drying agent rather than the commonly used silica gel which is able to exchange CO_2 (Long & Hallgren, 1985).

Photosynthetic rate was calculated using the difference in CO_2 concentration between air entering and air leaving the leaf chamber. In determing CO_2 concentrations, corrections were applied for the water vapour sensitivity of the IRGA. Since the LCA-2 did not incorporate optical filters to remove the response to water vapour, a further correction had to be applied for the change in CO_2 concentration with the change in chamber water

vapour concentration. Detailed equations for calculation of photosynthetic rate, transpiration rate and stomatal conductance are presented in the Appendix.

No detailed descriptions will be presented here of the approaches adopted for the gas exchange measurements of the various growth forms. Discussion thereof, together with considerations of the times at which measurements were to be performed are provided in section 3.7, where the outcome of preliminary studies are reported on.

3.4 METHODOLOGY TO DETERMINE THE PHOTOSYNTHETIC RESPONSE TO TEMPERATURE AND IRRADIANCE

Species selected for the investigation of photosynthetic responses to temperature and irradiance were Thamnochortus lucens, Erica plukenetii and Protea laurifolia (juvenile individuals). These species are representive of the three principal fynbos elements. Plants were transplanted with their original soil medium into separate 18-litre pots in June 1986. The potted plants were then put back into the soil and were left in their original surroundings for three months to establish. At the time when gas exchange measurements were to be performed, the individual potted plants were taken to the field station where plant CO_2 exchange measurements were performed under natural light conditions. Measurements were carried out during late spring (November 1986) and during late summer (February 1987).

Photosynthetic CO_2 exchange was monitored with a type 225 Mk3 infra-red gas analyser (Analytical Development Company Ltd., Hoddesdon, England). Since the analyser was fitted with an optical water vapour interference filter it was not necessary to compensate (by calculation) for the presence of water in the airstream. Photosynthetic rate was calculated using the

following equation (Long, 1982):

$$Pn = (V \times Diff)/A$$

where V = the flow rate of air through the assimilation chamber (200ml min^{-1})

Diff = the difference in CO_2 concentration before and after passing through the assimilation chamber

and A = Leaf Area

The layout of the measuring system is shown in Fig.3.13. Carbon dioxide uptake of the cuvette-enclosed plant material was measured in an open system as the difference between the inlet and outlet CO_2 concentration of an airstream passing through the cuvette. Air temperature and air humidity inside and outside the cuvette as well as PAR (photosynthetically active radiation) were recorded together with the rates of CO_2 exchange.

Two types of Perspex chambers were used. For single P.laurifolia leaves, a rectangularly shaped chamber (72 ml) was used. A longitudinal one (270 ml) was used for shoots of E.plukenetii and for the photosynthetic culms of T.lucens. Both chambers were temperature controlled by 2 water jackets through which water was circulated (see fig.3.1). Temperature was kept constant by changing the temperature of the circulating water and secondarily by altering the rate of water flow through the

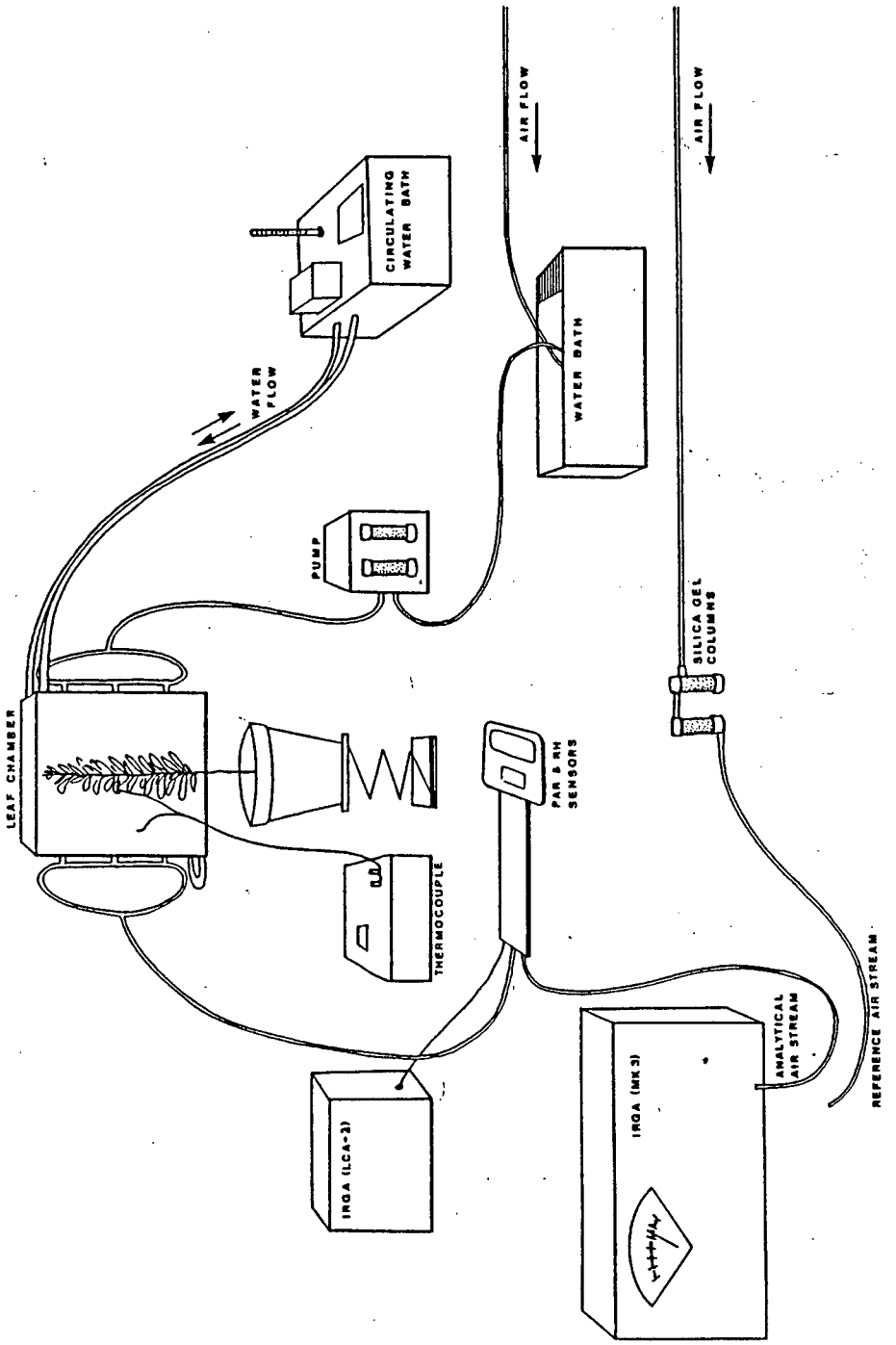


Fig.3.13: Layout of the measuring system used to determine the photosynthetic responses of selected fynbos species to temperature and irrigation.

water jackets.

Photon irradiance was measured with a selenium cell monitor with a filter providing response over 400 - 700 nm. The Parkinson Leaf Chamber (PLC, Analytical Development Company Ltd., Hoddesdon, England) was used to monitor humidity and PAR. Air temperature was monitored with a copper-constantin thermocouple. In all experiments ambient air was used.

The temperature in the cuvette was increased in steps of 10°C. Measurements were made from the lowest to the highest temperature and plants were allowed to equilibrate for 45 minutes after each temperature change. Plant material was then subjected to a range of light intensities by placing shade cloth between the assimilation chamber and direct sunlight. These commercially available shade cloths are generally used for horticultural purposes. Using cloths with different degrees of shading facilitated photosynthetic measurements at different light intensities. All measurements at each new light intensity were made after a steady rate of CO_2 exchange was obtained.

Absence of methodological means to regulate the water vapour concentration in the cuvettes necessitated operation of the system at low relative humidities. Relative humidity of the reference air was controlled using magnesium perchlorate columns on the air supply unit (ASU, Analytical Development Company Ltd., Hoddesdon, England). Measurements at low relative

humidities also prevented condensation on the inside of the chamber. Circulation of the air at high flow rates (400 $ml.min^{-1}$) kept the air space turbulent and reduced the boundary layer resistance in the chamber.

3.5 METHODOLOGY TO DETERMINE PHOTOSYNTHETIC RESPONSE TO IRRIGATION

The effect of irrigation on photosynthetic gas exchange was determined for the following species: Protea laurifolia, Erica plukenetii and Thamnochortus lucens. These species were chosen to be representative of the three principal fynbos elements i.e. proteoid, ericoid and restioid. The plant individuals were growing at the site described in section 3.1, they were of the same age (3 - 4 years old), and were therefore subject to similar atmospheric environmental conditions.

From 21 to 26 February 1987, 15 individuals of each species were irrigated with tap water. Each individual received one liter of water during the morning, at midday and during the late-afternoon. Gas exchange measurements were performed with the same measuring system described in section 3.3.

All gas exchange measurements were performed on 26 February 1987 at five to six time intervals during the day. Measurements were performed during cloudless conditions on 5 individuals each (at each time inetrval) of the unirrigated (control) and irrigated treatments of each species.

3.6 SEASONAL VEGETATIVE GROWTH STUDIES

One of the ultimate aims of this study was to relate the seasonal variations in carbon assimilation to some measure of plant performance. Periodicity of plant vegetative growth was considered as a measure of plant performance. Lack of standard phenological methods in ecological studies necessitated a subjective approach. Useful guidelines were provided by a recent synthesis of fynbos phenology studies (Pierce, 1984).

Methods employed were non-destructive. Observations were taken at one-month intervals from September 1985 to February 1987. The length of the study period provided a field knowledge of the species which proved to be valuable in the assessment of the various phenophases. Monthly measurements were taken of the increments in lengths of labelled shoots. Five to eight shoots were labelled in September 1985. New shoots were lebelled every month since then. These were included in the existing sample to replace lost labels and to avoid possible erroneous observations due to the effect of the label on growth of the tagged plant. Towards the middle of the study period, the sample size was maintained at 10 - 15 shoots per species. Tags were made to be loose-fitting, light in weight and as inconspicuous as possible. Tags were placed around the bases of emerging culms of the restiod species at the time of culm development (August - September). For the other species, tags were attached loosely to the bases of randomly chosen stems.

3.7 PRELIMINARY STUDIES

3.7.1 Introduction

Before embarking on a full-scale monthly program of field studies, exploratory studies were undertaken to enable the design of an experimental program, i.e. when, where and how readings were to be taken. Emphasis was placed on quantitative assessments of the degree of diurnal variation in photosynthetic behaviour with respect to leaf age and position, micro-environmental differences and changes in ambient climatic conditions.

A first priority was to identify the photosynthesizing regions of the plant that would best represent the maximum photosynthetic activity at any particular time. To this aim, individual species were investigated to establish the degree of variation in transpiration and photosynthetic rates with leaf age, orientation and position on plants. These studies facilitated the identification of classes of tissue (eg. age classes) which exhibit the same physiological activity. Leaves (or internodes for the restioids) of the same "physiological class" with the least inherent variation and with the same orientation were then selected for intensive investigation throughout the study period.

These initial studies also included the determination of the variation in the rates of photosynthetic gas exchange throughout the course of the day. The effects of transitory changes in the prevailing environmental conditions on the rates of C-fixation were also investigated. In this study, sudden gusts of wind, momentary shading by a passing cloud, leaf detachment from plant and extended periods of sampling time were all considered as transitory alterations to the prevailing conditions.

3.7.2 Results and Discussion of Preliminary studies

The rates of photosynthesis were determined for leaves of different age on the following broad-leaf species: Protea laurifolia, Metrosideros angustifolia, and Leucadendron salignum. The leaves of all species attained their maximum photosynthetic capacity approximately at the time of apparent leaf maturity during the first season of growth. For these species it was possible to determine plant age by counting the number of internodes on the stem. Beginning during the second year of age, the rate of net photosynthesis decreased slowly with increasing age of the leaves.

In a study of the photosynthetic behaviour of the most recently matured leaves, it was found that leaf position on the stem had a remarkable effect on leaf photosynthesis. The second to the fourth pairs of leaves of P.laurifolia showed very little

variation in photosynthetic rates throughout the day (Table 3.1). The first (very young) and fifth pairs of leaves, however, always exhibited lower photosynthetic rates. The different photosynthetic rates in relation to position on stem were determined under full sunlight conditions as well on cloudy days.

On clear days the leaves in the shade of the canopy exhibited photosynthetic rates comparable to the rates experienced by exposed leaves on cloudy days. These readings obtained for shaded leaves were variable with no clear pattern of photosyntetic rates in terms of position on stem. On the basis of these results, it was decided that all subsequent measurements intended for the seasonal study of C-fixation in P.laurifolia should be performed exclusively on the second to the fourth pairs of leaves. The elevated photosynthetic rates of these leaves are probably related to differing allocation patterns of water and nutrients to the various pairs of leaves since the first and fifth pairs of leaves were almost always smaller and more leathery in nature.

Similarly, the most recently matured basal and apex leaves of M.angustifolia were not included in the intended seasonal study because of their depressed and variable photosynthetic rates (Table 3.2). Transpiration rates of the apex leaves were comparable to the rates obtained for intermediate leaves but

Table 3.1: Variation in net photosynthetic rate ($mgCO_2\ dm^{-2}\ h^{-1}$) of P.laurifolia with position on plant.

	HIGH PAR			LOW PAR	SHADE
	morning	midday	late-aft.	midday	midday
P1	15,41	7,56	12,89	2,11	3,85
P2	17,17	15,82	16,73	4,45	4,63
P3	17,56	16,19	17,05	3,28	3,81
P4	17,75	16,19	17,11	3,86	5,52
P5	17,18	9,09	14,62	1,91	2,48

Readings were taken on 5 September 1985 under cloudless conditions on fully exposed leaves (HIGH PAR) and on shaded leaves (SHADE). Measurements were also performed under cloudy conditions (LOW PAR) on 7 September 1985. "P" denotes the pair of leaves, e.g. P1 represents the first pair of leaves. The values in the table are the means of 5 replicate measurements. The highest calculated standard error of the mean (SEM) was 0,8.

Table 3.2: Variation in net photosynthetic rate ($mgCO_2\ dm^{-2}\ h^{-1}$) and transpiration rate ($mgH_2O\ dm^{-2}\ s^{-1}$) of M.angustifolia.

Leaf Position	Net Photosynthetic Rate	Transpiration Rate
Intermediate	17,256 ± 0,387	1,022 ± 0,038
Basal	10,409 ± 0,531	0,785 ± 0,008
Apex	11,997 ± 0,665	1,102 ± 0,015

Measurements were performed on 4 September 1985 at midday. Results are expressed as means (± standard error of the mean) of 5 replicate measurements.

were significantly higher than rates exhibited by basal leaves. Anatomical investigations of M.angustifolia revealed that only the abaxial surfaces have stomata. The abaxial leaf surfaces were always orientated away from the sun.

Only the leaves of the female individuals of L.salignum were considered for gas exchange measurements since they were almost always bigger in size and they showed higher photosynthetic capacities than the leaves of the male plants. The green inflorescence bracts around the bases of the male and female cones did not have consistent rates of net photosynthesis and were mostly lower than the rates obtained for the mature vegetative leaves.

A major drawback of the Parkinson's leaf chamber was that the design was only practical for operation on petiolated leaves. Measurements on sessile leaves, like L.saligna allowed only part of the leaf to be in the chamber and this always resulted in damage to surrounding leaves. Readings on detached leaves of L.saligna, however, showed that there was no change in rates of photosynthetic gas exchange of such a leaf within five minutes after detachment. The cut end of the leaf had to be sealed with vaseline to prevent excessive water loss which could result in erroneous humidity readings and consequently the determination of incorrect transpiration rates. Leaves of P.laurifolia seedlings at the 3 - 3,5 years of age occurred in clusters and

did not have the paired nature of the older individuals. Within such a cluster of most recently matured leaves there were always some poorly developed ones near the apex. Only the better developed leaves were considered for monthly gas exchange measurements. Moreover, the most recently developed leaves were always bigger than the leaves of the previous season's growth. This resulted in the latter almost always being in the shade and were consequently not included as study material to record the monthly maximum photosynthetic potential.

Different internodes of the photosynthetic culms of Thamnochortus lucens and Askidiosperma paniculatum did not exhibit marked differences in photosynthetic rates when they were fully exposed to the sun. The fourth to the last internodes below the inflorescence, however, were occasionally shaded by the other culms. Because of the uncertainty of the photosynthetic response of these internodes to occasional exposure to the sun, it was decided not to use them for monthly gas exchange recordings.

The ericoid species, Erica plukenetii and Erica hispidula, with their unique plant architecture, demanded a totally different approach for their gas exchange measurements. These low, evergreen shrubs have hard, narrow and rolled leaves. On the abaxial surfaces of these small leaves are non-photosynthetic hairy grooves where the stomata are found.

The shoots of these species were found suitable for gas exchange measurements using the PLC. Suitability can be interpreted here as not causing leaks in the air circuit at the point of insertion in the chamber. It also defines the non-injurious nature of such measurements. The usage of entire shoots as areas of gas exchange in the PLC presented a problem in that flowers are also borne on the shoots. This could result in an underestimation of photosynthetic rates since the reproductive structures release considerable amounts of CO_2 by means of respiration. When single flowers were placed in the PLC it was found that they do have an appreciable respiratory potential. It is also of interest that the developing flowers released higher amounts of CO_2 in the analytical airstream than the mature flowers. It was then reasoned that removal of flowers from the shoot prior to gas exchange measurements would result in excessive water loss through the broken pedicels. This was found not be the case. Removal of one up to ten flowers in a step-wise fashion with concomitant gas exchange measurements (allowing for recovery between readings) did not show the expected increases in transpiration rates with increasing number of flowers being removed.

It was originally intended to express photosynthetic or transpirational activity for all species as net CO_2 or H_2O exchange per unit leaf area per unit time. For the broad-leaf species, the conventional approach was adopted of using the area of one leaf surface as the photosynthesizing area to be entered

in the appropriate formula. The photosynthetic culms of the restioids were treated as cylinders and the areas calculated accordingly.

The ericoid leaves, however, presented a problem in that generalized methods of leaf area determinations could not be easily applied. A number of different techniques were initially used to estimate ericoid leaf area. The percentage error in using these methods was considered too large for the accuracy level at which it was intended to calculate rates of photosynthetic gas exchange. The most promising method employed was a technique which took advantage of the correlation between projected leaf surface areas and light intensity (Mitchell, 1936; Kramer, 1937). This method was based on the principle that light intensity reaching a detector from a constant source is proportional to the leaf area placed between the detector and the light source. A further relationship between the true leaf area - taking geometric shape and abaxial groove into consideration - and the projected leaf area facilitated the determination of the aggregate surface area of a large sample of detached ericoid leaves. This attempt, however, was soon abandoned because of its elaborate and time-consuming nature.

The eventual outcome of these attempts to estimate ericoid leaf area was the decision to express ericoid gas exchange rates on a

unit dry weight basis. It could be argued that this approach would not allow comparisons between measuments of ericoid species and those of the restioid and proteoid species. The major concern, however, was to understand the relative changes in gas exchange parameters and their relations with changes in the environment. In other words, comparisons of patterns of gas exchange was considered as being of greater importance than comparisons of absolute rates of gas exchange. Such an approach was considered necessary to allow speculation about adaptive physiology and its ecological implications in the different growth forms.

A major advantage of these preliminary studies was the resultant ability to identify precautionary measures which would ensure the comparability of all monthly recordings. For example: it was established that comparative carbon fixation measurements would only be performed under cloudless conditions. Reasons for taking this precaution were manifold. Firstly, because of the dependence of photosynthetic rate on the level of irradiance and, secondly , because of the fluctuating light intensity experienced during a cloudy day. Furthermore, experimental evidence for adaptations of entire photosynthetic systems to a particular light regime (Mahall & Schlesinger, 1982) could also be relevant for fynbos species. Lastly, different degrees of cloud cover would result in inconsistent light regimes during different months and this would complicate comparative interpretation of photosynthetic behaviour.

Preliminary investigations of diurnal variations in gas exchange indicated the time at which measurements were to be taken. Morning readings were to performed about one hour after sunrise, midday readings around noon and late-afternoon measurements were to be taken one hour before sunset. It was reasoned that this pattern of measurements would sample the daily variation more accurately than performing readings at set times o'clock throughout the year.

CHAPTER 4:

RESULTS and DISCUSSION

4.1 SEASONAL PROGRESSION AND DIURNAL VARIATION IN XYLEM PRESSURE POTENTIALS

The xylem pressure potentials of the seven species described in section 3.1 were measured with the pressure chamber. Pre-dawn and midday measurements were taken from January to December 1986. The results are presented as the averages of 4 to 6 measurements, and are shown in figures 4.1 to 4.8. Although all the species studied were growing at the same site, the magnitudes of seasonal and diurnal changes in xylem pressure potentials differed for each species.

Diurnal Patterns

Generally, xylem pressure potentials of each species decreased from pre-dawn to midday (figs.4.1 - 4.8). The pre-dawn potentials were usually higher (less negative) because water uptake continued at night without the high transpirational water loss which the plants experience during the day. Although water uptake may be slower at night because of lower temperatures, the xylem pressure potentials do reach the highest values allowed by the equilibrium processes with the soil water (Miller, 1985).

During July, some species exhibited an inversion of the general diurnal pattern of xylem pressure potentials in that the potentials of these species were slightly higher in the middle of the day than at pre-dawn. This anomalous pattern was found in the young and mature individuals of Protea laurifolia (figs. 4.5 & 4.6) and in Leucadendron salignum (fig.4.7). A similar `inversion' was reported for Larrea tridentata growing in New Mexico (Syvertsen et al.,1975) and for the fynbos species, Rhus incisa, Rhus dissecta, and Eriocephalus africanus (Miller, 1985). The diurnal changes in soil and air temperatures, the relatively extensive rooting systems of these species and the saturating soil moisture conditions at that time of the year can probably account for the higher midday xylem pressure potentials. The elevated daytime soil temperatures, in contrast to the much reduced values during the night, could have resulted in more efficient water uptake processes.

Unfortunately, estimates of soil water content were not recorded. Estimates like soil water potential provide a useful index of soil water availability which could be used to interpret seasonal variation in xylem pressure potentials. Sommerville (1983), for example, related xylem potentials with gravimetric soil moisture data. For the present study, monthly average rainfall data was used as an indication of water availability.

Seasonal patterns

For all species the lowest xylem pressure potentials were recorded during the spring and summer months (figs.4.1 to 4.8). This seasonal pattern corresponds well with the monthly variation in precipitation with the lowest potentials measured at the time of lowest rainfall. The magnitudes of the seasonal variations in xylem pressure potentials are comparable to values obtained for fynbos species by Miller et al.(1983), Miller et al.(1984), Miller (1985) and Sommerville (1983). The values also correspond with xylem pressure potential measurements of several mediterranean-climate sclerophyllous species (Poole & Miller, 1975; Poole & Miller,1978; Miller & Poole,1979).

At the start of the study period, in January, the xylem pressure potentials of all species were generally low. From February onwards, a general increase in xylem pressure potentials were experienced for all species at both times of the day. This increase in potentials was probably in response to water becoming more readily available with the increase in periodicity of rainfall. Between April and September the pre-dawn xylem pressure potentials were mostly constant. The midday potentials, however, showed a greater degree of variation during this period but the difference between two consecutive monthly readings for each species was always within a range of 10 bars. Furthermore, these potentials never reached the low values recorded during the summer months. A decrease in xylem pressure potentials was again experienced towards October and November for most

species. This decrease in potentials also marked the onset of the period of assumed water stress.

Deep-rooted species

The highest xylem pressure potentials thoughout the study period were experienced by the seedlings and mature individuals of Protea laurifolia (figs.4.5 & 4.6), by Metrosideros angustifolia (fig.4.8) and by Leucadendron salignum (fig.4.7). These species also exhibited the least diurnal variations in xylem pressure potentials. The deeper and more extensive rooting systems of these species could possibly account for the generally higher xylem pressure potentials. Their rooting systems are able to penetrate deeper soil depths thereby tapping water sources which are unavailable to the shallow-rooted species. Rooting depth was used by Sommerville (1983) to partially explain observed differences in magnitude of xylem pressure potentials of Thamnochortus punctatus and Leucospermum parile. Similarly, Poole & Miller (1975) related differences in pressure potentials of Californian evergreen shrubs to rooting habit.

The pre-dawn potentials of the deep-rooted species were generally high with recorded values always being less than -6 bars throughout the study period (figs. 4.5 - 4.8). The midday xylem pressure potentials of these species were low during the first three to four months, marking the months of generally lower rainfall. The midday potentials from May to

September were higher, presumably because of increased soil water levels. The mature individuals (fig.4.5) and the seedlings (fig.4.6) of P.laurifolia experienced decreases in midday potentials from October onwards and reached their lowest values in November. The midday xylem pressure potentials of L.salignum (fig.4.7) also decreased from October but only reached a minimum value of -13 bars in December. M.angustifolia (fig.4.8) did not experience dramatic decreases in potentials during spring.

Although the general seasonal patterns of midday xylem pressure potentials of the deep-rooted species were comparable, slight differences were apparent with respect to the magnitudes reached and with respect to the month of occurrence of lowest potentials. These differences can possibly be accounted for by growth habit or habitat. For example, M.angustifolia which is found along stream banks, could possibly have had soil water available at times when the other deep-rooted species were already subjected to summer water shortage. This could explain the maintenance of constant and high xylem pressure potentials over a longer period of the year (fig.4.8).

L.saligna (fig.4.7) exhibited persistantly higher xpp levels than those of P.laurifolia (figs. 4.5 & 4.6) during the summer months. This suggests that L.saligna was much better supplied with soil water than the juvenile and mature individuals of P.laurifolia. The lower levels of water stress encountered by

L.saligna must be attributed to the fact that measurements were performed on individuals which had resprouted after a fire in 1982. In contrast, P.laurifolia, a reseeder, did not have the advantage of an established rooting system. The resprouting charateristic ensured that L.saligna was well supplied with soil water throughout the year.

Shallow-rooted species

On the basis of depth and extent of rooting systems the following species can be considered as being shallow-rooted: Thamnochortus lucens, Askidiosperma paniculatum, Erica hispidula and Erica plukenetii. All of these species experienced dramatic shifts in their monthly xylem pressure potentials. During January and December the pre-dawn potentials were the lowest coinciding with the period of lowest monthly rainfall. During the summer period, decreases in pre-dawn xylem pressure potentials were the most marked for T.lucens (fig.4.3) for which an average potential of -30 bar was recorded in January and an average potential of -40 bar in December. The lowest pre-dawn potentials recorded for the ericoid species (figs.4.1 & 4.2) and for A.paniculatum (fig.4.4) were between -15 and -25 bars. These low pre-dawn potentials of the shallow-rooted species during January and December indicate that limited soil water was available to allow overnight recovery of plant water status.

The midday xylem pressure potentials of the shallow-rooted

species exhibited even more dramatic monthly variations. The lowest potentials (-40 bar) were recorded for T.lucens (fig.4.3) during January and February of 1986. These values were lower than the potentials recorded for A.paniculatum (fig.4.4) which experienced xylem pressure potentials of -24 and -31 bars respectively during November and January of 1986. The differences in magnitude and in the time (month) of lowest recorded potentials of the two restioid species suggests that xylem pressure potential is not controlled by a single factor like root depth. Both ericoid species (figs.4.1 & 4.2) experienced minimum potentials comparable to the values observed for T.lucens during January and December.

All shallow-rooted species experienced increases in midday xylem pressure potentials during February, presumably in response to more soil water being available in the upper soil horizons. Although the midday potentials recorded for all shallow-rooted species from March to October were always less than -20 bars, differences in the monthly patterns were apparent. For example, all species except T.lucens (fig.4.3) experienced an increase in xylem potential from August to September. It is likely that drought adaptations such as leaf size and anatomy could have contributed to the variations in the patterns of pressure potentials over this period.

The irregular pattern of midday xylem pressure potentials from March to October was evident for both the shallow-rooted and the

deep-rooted species. The irregularity, however, was most marked for the shallow-rooted species. The variation during this period could be attributed to varying levels of soil moisture which in turn was influenced by sampling date. The desirable approach would have been to maintain a constant interval between the date of measurements and the day of last rains. This was not possible, however, since the primary objective of the study was to obtain concurrent measurements of rates of carbon assimilation and plant water status. Furthermore, measurements of carbon assimilation were taken on cloudless days to reduce the effect of varying light intensity. Since cloudless conditions did not occur very often over the winter period, xylem pressure potential and C-fixation measurements had to be made irrespective of the number of days following rain. The resulting different monthly levels of soil moisture influenced xylem pressure potentials accordingly and hence the irregular pattern from March to October.

Each value in the figure series 4.1 to 4.8 is the mean of 6 replicate measurements and the corresponding vertical bar represents the standard error of the mean (SEM). The absence of a vertical bar signifies that the SEM is too small to show on the scale of the figure.

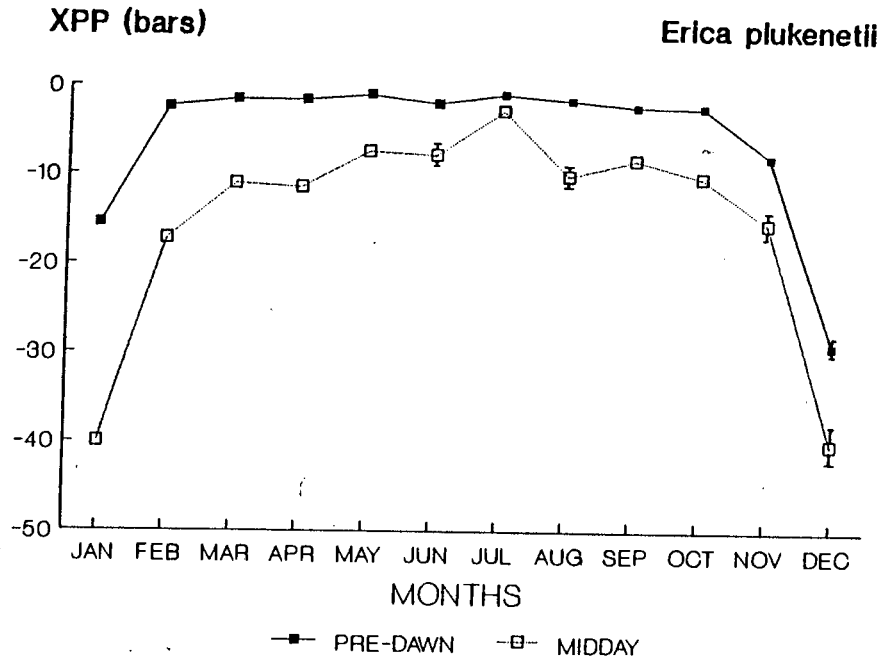


Fig.4.1: Seasonal course of midday and pre-dawn xylem pressure potential of Erica plukenetii from January to December 1986.

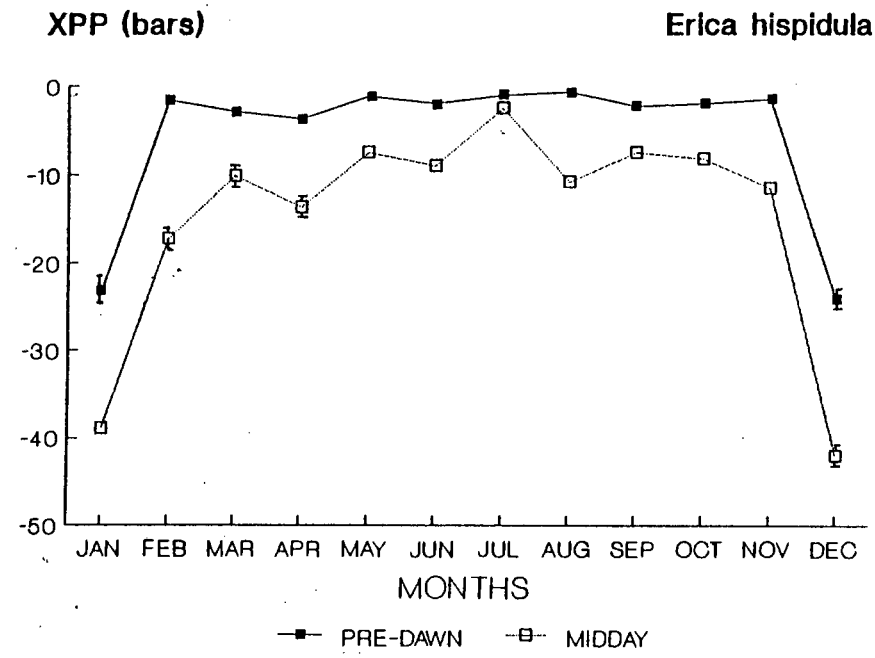


Fig.4.2: Seasonal course of midday and pre-dawn xylem pressure potential of Erica hispidula from January to December 1986.

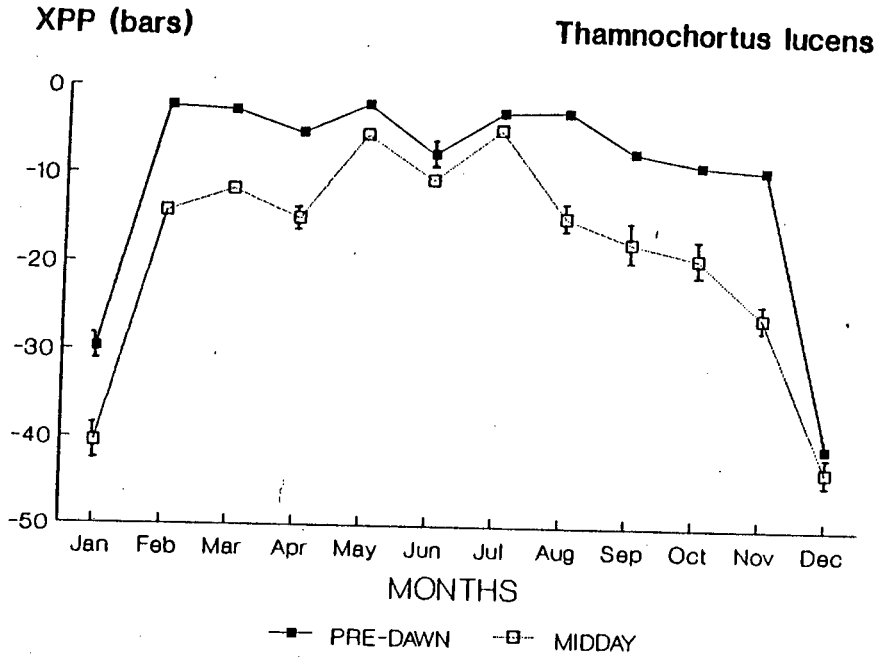


Fig.4.3: Seasonal course of midday and pre-dawn xylem pressure potential of Thamnochortus lucens from January to December 1986.

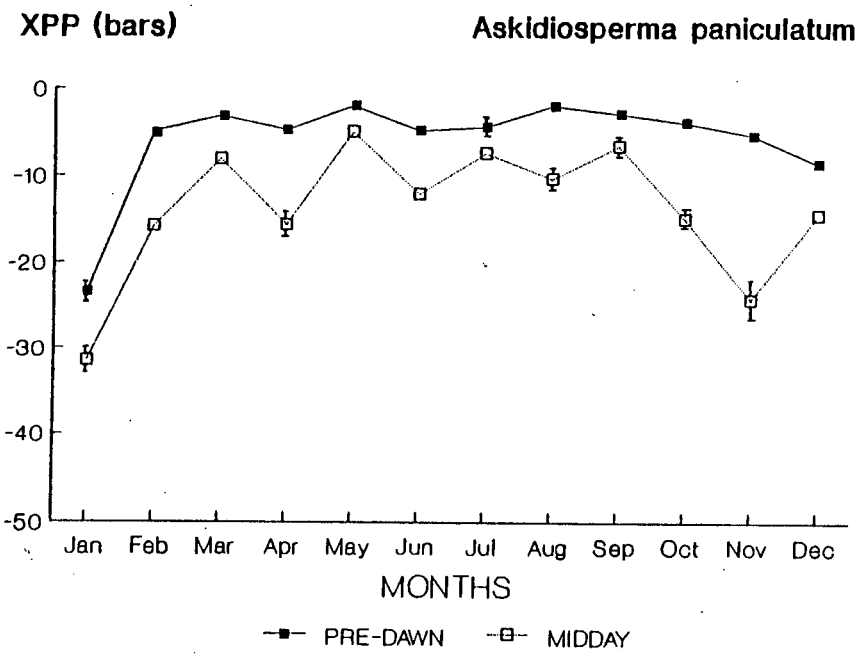


Fig.4.4: Seasonal course of midday and pre-dawn xylem pressure potential of Askidiosperma paniculatum from January to December 1986.

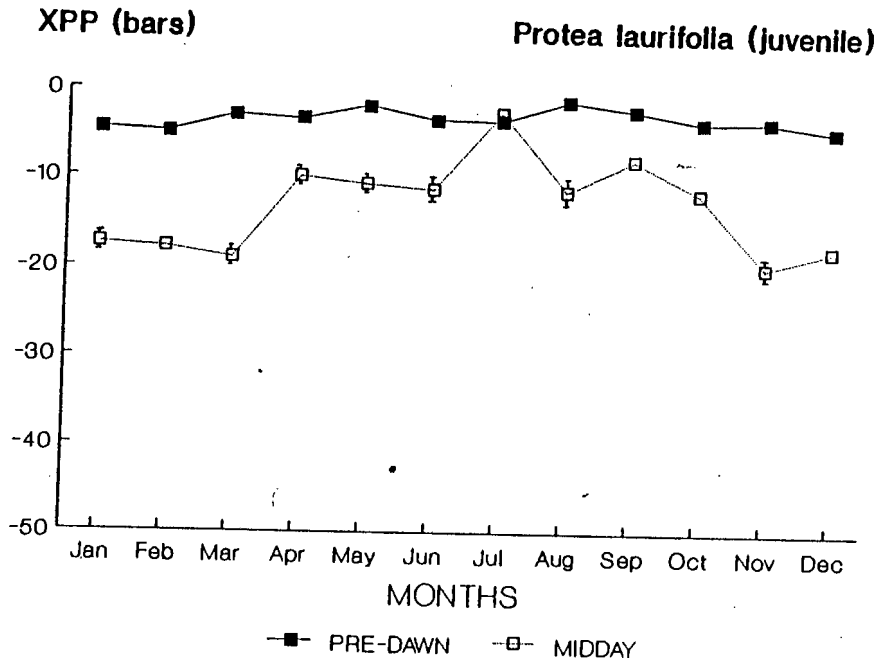


Fig.4.5: Seasonal course of midday and pre-dawn xylem pressure potential of Protea laurifolia (seedling) from January to December 1986.

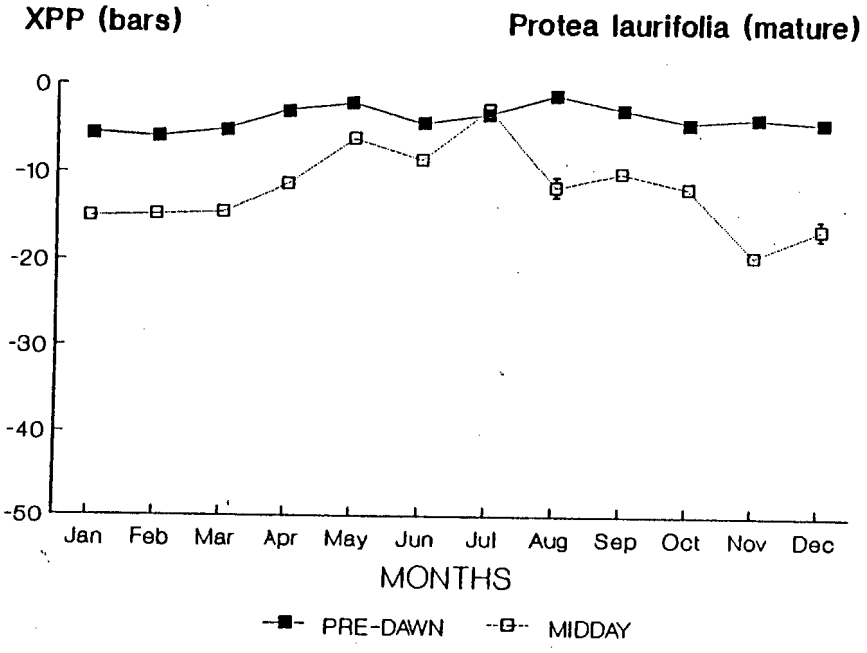


Fig.4.6: Seasonal course of midday and pre-dawn xylem pressure potential of Protea laurifolia (mature) from January to December 1986.

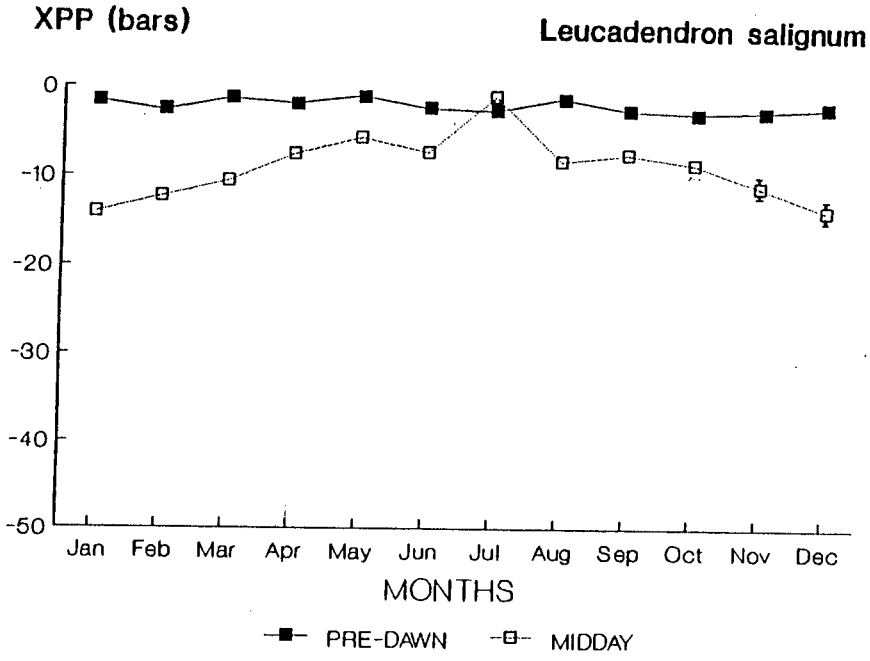


Fig.4.7: Seasonal course of midday and pre-dawn xylem pressure potential of Leucadendron salignum from January to December 1986.

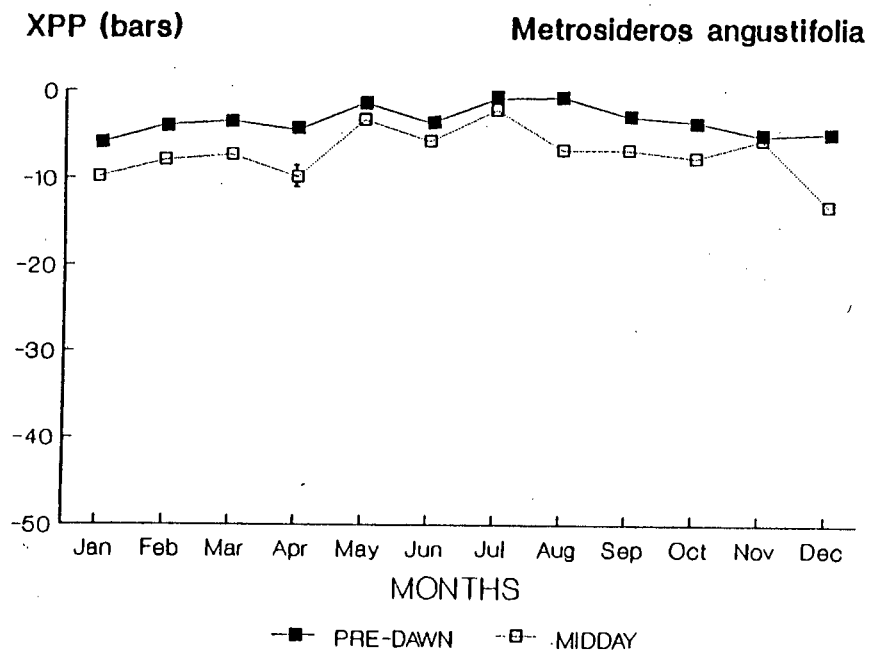


Fig.4.8: Seasonal course of midday and pre-dawn xylem pressure potential of Metrosideros angustifolia from January to December 1986.

4.2 SEASONAL PROGRESSION AND DIURNAL VARIATION IN RATES OF PHOTOSYNTHETIC GAS EXCHANGE

Field measurements to determine the rates of photosynthetic gas exchange of the seven mountain fynbos species were performed at one-month intervals from January to December 1986. The term 'photosynthetic gas exchange', as it is used here, encompasses net photosynthetic rate (Pn) and stomatal conductance (Gs). Transpiration rate (Tr) was measured concurrently with Pn and Gs. The seasonal progression and diurnal variation in transpiration rate of the seven mountain fynbos species studied are presented and discussed in section 4.3. The measuring techniques used to determine net photosynthetic rate, stomatal conductance and transpiration rate were described in section 3.3. Equations used for the calculation of these physiological rates of activity are presented in the Appendix. Transpiration ratio (TR) (Helmuth, 1971), was also calculated and was used as a measure of the efficiency of water usage during photosynthesis. TR is expressed using the following quotient: transpiration rate/net photosynthetic rate. The equations used for the calculation of TR are set out in the Appendix. The calculated TR values are reported on in section 4.4.

Attempts are made to provide a physiological basis for

understanding the observed seasonal changes in rates of photosynthetic gas exchange. The adaptive significance thereof will also be considered. To this end, the possible relationships between plant water status and the rates of photosynthetic gas exchange (Pn and Gs) will be assessed. Midday Pn and Gs are considered primarily because measurements at this time of the day were performed concurrently with xpp determinations.

Numerous studies have shown that photosynthetic response to diurnal changes in environmental factors are species-specific (Lange et al., 1982; Roesler & Monson, 1985; Tenhunen et al., 1982). These studies have highlighted the facts that environmental factors are interdependent in eliciting a particular photosynthetic behaviour, and also that non-stomatal factors contribute to some extent to the observed patterns of photosynthetic gas exchange. Too little is presently known to adequately explain the mechanisms which control these physiological processes. This lack of understanding of the sensitivity of fynbos photosynthetic gas exchange processes to immediate changes in atmospheric environmental factors prevents a thorough analysis of observed diurnal changes in photosynthetic gas exchange. The measured diurnal changes in Pn and Gs from January to December are therefore not discussed in great detail but are graphically illustrated at the end of this section.

Regression analysis (Statgraphics, 1986) are used to quantify the nature and the strength of the relationships among variables. This statistical procedure provides a basis for explaining some of the observed seasonal gas exchange patterns.

Since attempts failed to develop a quick method of estimating ericoid leaf area (refer to section 3.7), the rates of photosynthetic gas exchange of the ericoid species are expressed on a unit dry weight basis. In contrast, results for the restioid and the broad-leaf species are expressed on a unit leaf area basis. A direct comparison between the net photosynthetic rates of the three major fynbos growth forms is provided in Chapter 5.

Each value in the figure series 4.9 to 4.25 is the mean of 6 replicate measurements and the corresponding vertical bar represents the standard error of the mean. Where there are no vertical bars, the standard error of the mean is too small to show on the scale of the graph.

4.2.1 ERICOID SPECIES

The remarkable feature of the seasonal course of photosynthetic gas exchange is that the gradual decreases in Pn and Gs towards the end of summer were accompanied by more negative xylem pressure potentials (figs. 4.9 & 4.10). It is tempting to

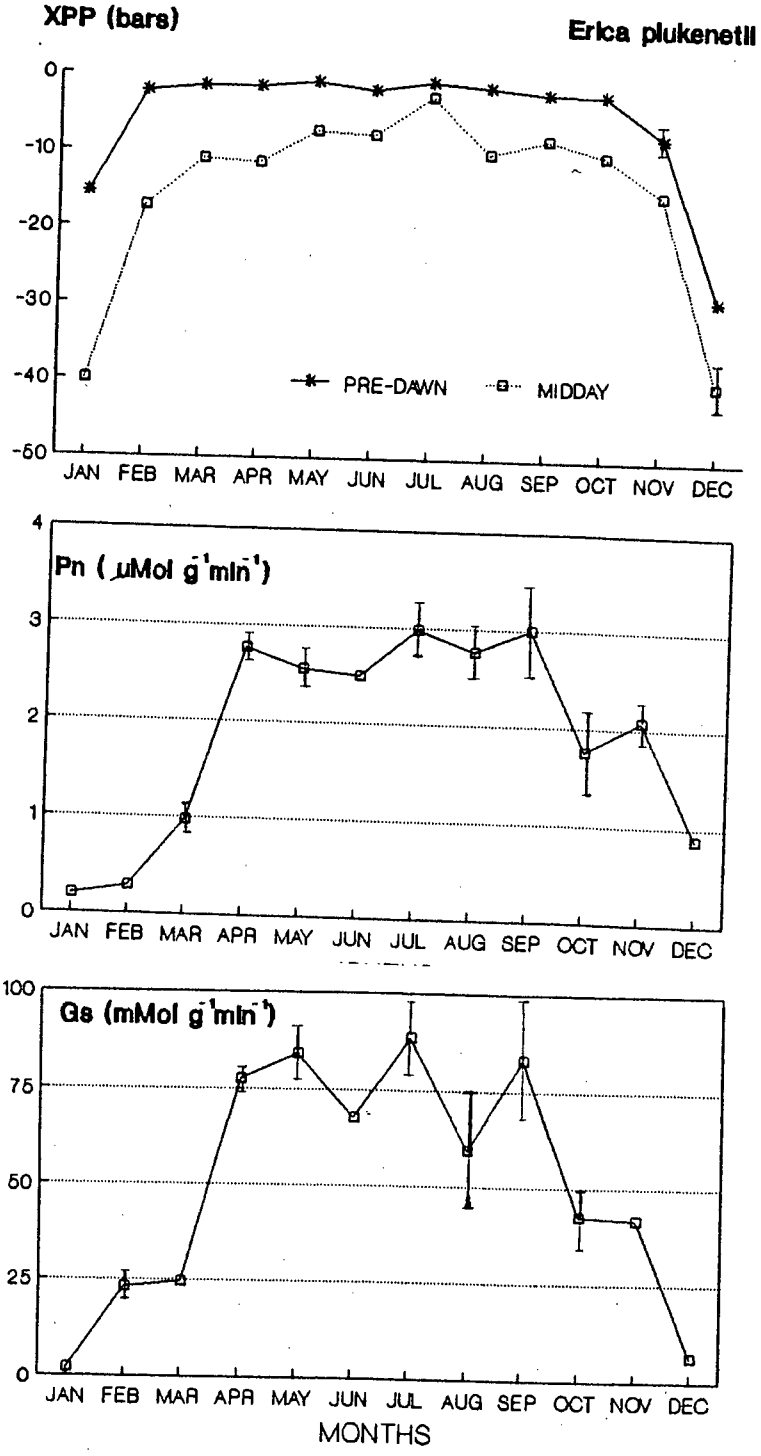


Figure 4.9: Seasonal course of xylem pressure potential (xpp), midday net photosynthetic rate (Pn) and midday stomatal conductance (Gs) of Erica plukenetii from January to December 1986.

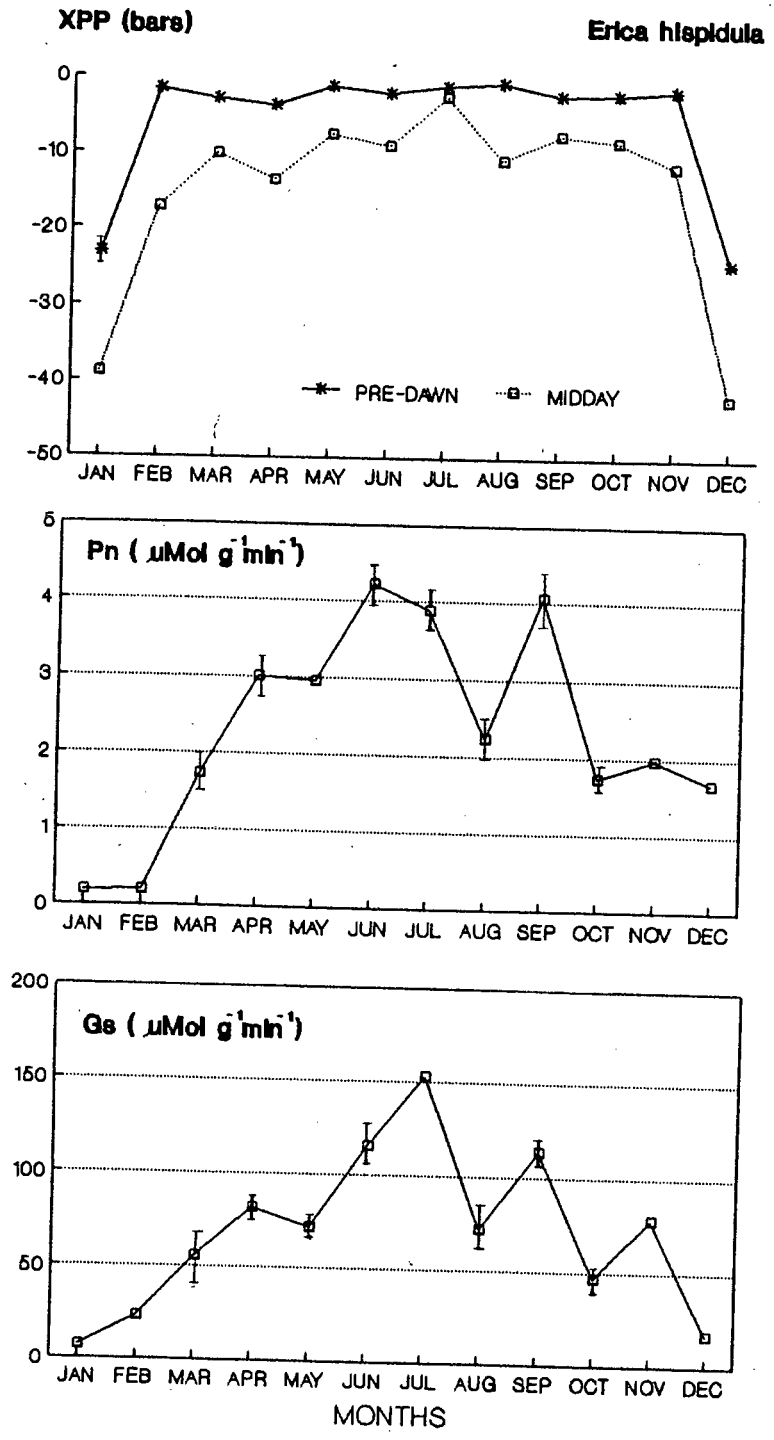


Figure 4.10: Seasonal course of xylem pressure potential (xpp), midday net photosynthetic rate (Pn) and midday stomatal conductance (Gs) of Erica hispidula from January to December 1986.

suggest that the decrease in plant water status observed as less negative xylem pressure potentials from October to February acted as the physiological signal for partial stomatal closure resulting in decreased stomatal conductances and consequently decreased rates of net photosynthesis. However, the expected correlation between Pn and xpp is lacking: statistical analysis showed that for both ericoid species there was no significant correlation between xpp and Pn (Appendix Table 1). On the other hand, highly significant correlations between Gs and xpp were found (Appendix Table 1).

The lack of correlation between plant water status and net photosynthetic rate of the ericoid species is also apparent when the diurnal courses of Pn are analysed. The diurnal Pn pattern of Erica plukenetii (fig.4.11) observed during early summer (December) was markedly different from the pattern observed during late summer (February). During December, when a mean midday xylem pressure potential of -40 bars was recorded, a mean midday net photosynthetic rate of 0.879 μMol g^{-1} min^{-1} was measured with a recovery in Pn to 1.25 μMol g^{-1} min^{-1} in the late-afternoon. During February (late-summer), however, midday xpp was -17 bars, midday Pn was 0.288 μMol g^{-1} min^{-1} and decreasing even further in the late-afternoon. Although there was an improvement in plant water status from December to February at the time when measurements were taken, Pn decreased and the diurnal pattern of Pn changed from one of a midday

depression to one of a gradual decrease throughout the day.

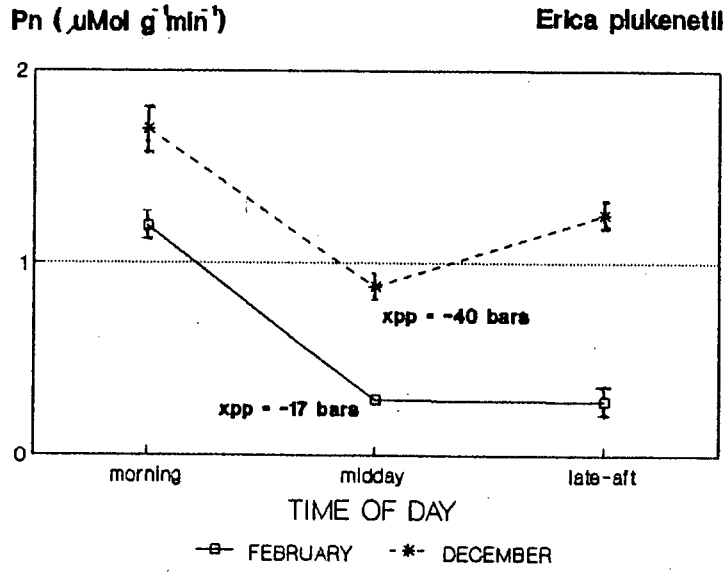


Fig. 4.11: Diurnal patterns of net photosynthetic rate (Pn) of Erica plukenetii during February and December.

The decrease in net photosynthetic rate from December to February accompanied by the improvement of plant water status lends support to findings by Gigon (1979) that for some species the water factor cannot be considered as the overriding factor determining the seasonal decline in the rate of photosynthetic C-fixation.

It is possible that the higher temperatures generally experienced

during January and February (refer to section 3.1) could have been the causative factor for the summer reduction in net photosynthesis. Photosynthetic temperature response studies (section 4.3) indeed showed a decrease in net photosynthetic rate of E.plukenetii when temperatures approached 30°C. It is also likely that the unique morphological and anatomical features of the ericoid leaves (refer to section 3.7) could also have delayed the onset of plant physiological response to the decreased plant water status experienced during December. Recent evidence from studies on other Mediterranean-type sclerophylls have shown that factors like temperature and humidity (Lange et al., 1982) could have stronger influence on stomatal movements than plant water status alone.

For both E.plukenetii and E.hispidula more or less parallel patterns were found for the seasonal progression of net photosynthesis and stomatal conductance. These comparable patterns suggest that seasonal changes in environmental factors cause strongly similar seasonal changes in gas exchange characteristics of E.plukenetii and E.hispidula. However, the absolute values recorded for each species were not always of the same magnitude. While the photsynthetic rates of E.plukenetii (fig. 4.9) and of E.hispidula (fig.4.10) were almost always comparable, the stomatal conductances of E.hispidula were often as much as twice the values recorded for E.plukenetii. These

differences may have been caused by the method used whereby numerous leaves on an entire stem were put in the assimilation chamber. Since the arrangement and the density of the leaves on the stems of the two species differed markedly, the flow dynamics in the assimilation chamber could have been affected, resulting in estimates deviating from the true values. Alternatively, it could also be argued that the differences in leaf density of the two species resulted in different microclimates on the leaf surfaces which possibly resulted in dissimilar stomatal behavioural patterns in response to changing environmental factors.

4.2.2 RESTIOID SPECIES

The seasonal patterns of photosynthetic gas exchange of the restioid and ericoid species exhibited some common features. Firstly, lowest Pn and lowest Gs (figs.4.12 & 4.13) of the restioid species were also recorded from the late-spring to summer months. The rates of decline in gas exchange values from the maximum during September to the minimum during summer (January) were also similar for both the ericoid and restioid growth forms. For example, the midday Pn of Thamnochortus lucens (fig.4.12) increased by 97% from January to September while that of E.plukenetii (fig.4.9) increased by 94% over the same period. Because water shortage is such a distinctive feature of mediterranean-climate summers, it appears reasonable to associate any observed decreases in physiological activity during this period with the effects of summer drought. Both growth forms experienced low xpp's during the late-spring to summer period (section 4.1) and the severity of water stress encountered are explained on the basis of the depth and extent of their rooting systems. A similar relationship between gas exchange patterns and season of year has also been noted for numerous plants from other ecosystems and in many cases these relationships were attributed to the effects of water shortage during summer on

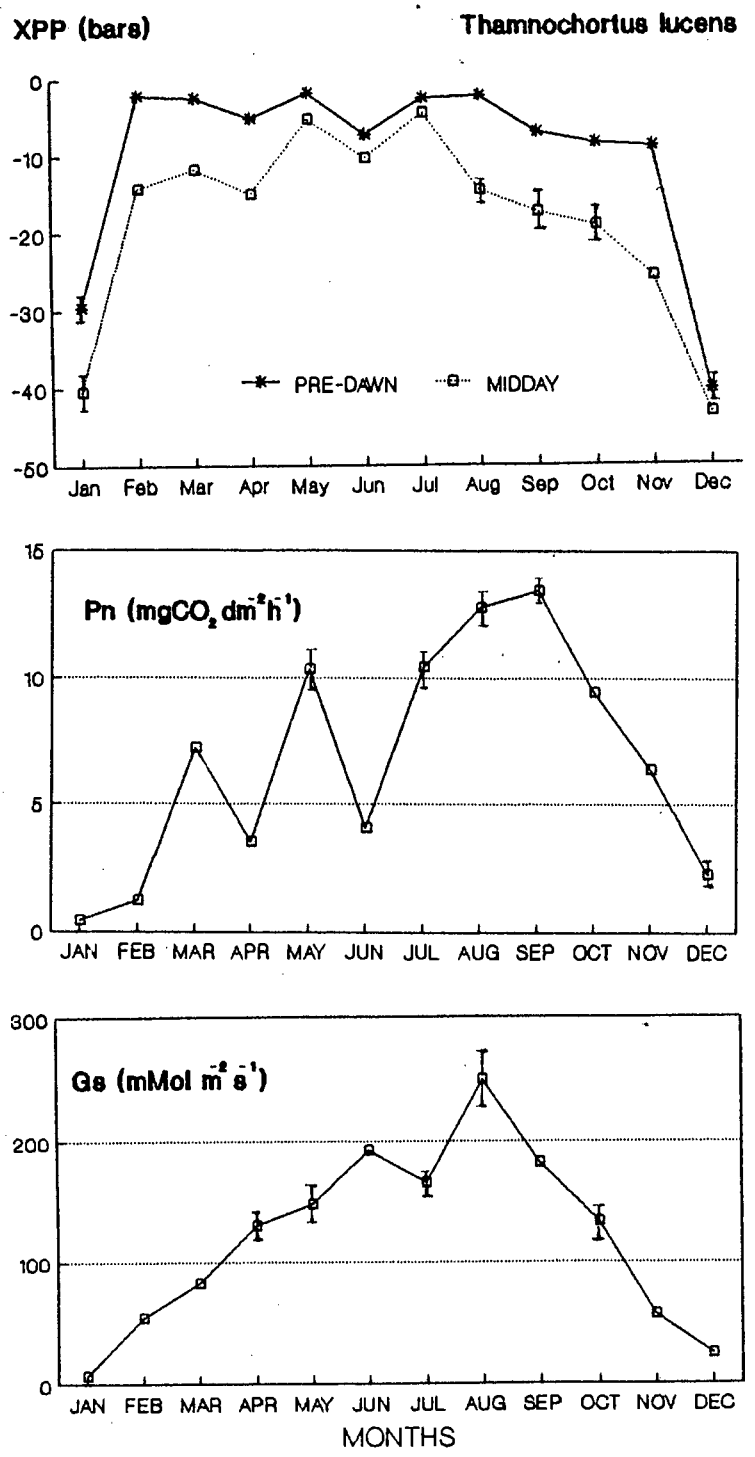


Fig.4.12: Seasonal course of xylem pressure potential (xpp), midday net photosynthetic rate (Pn) and midday stomatal conductance (Gs) of Thamnochortus lucens from January to December 1986.

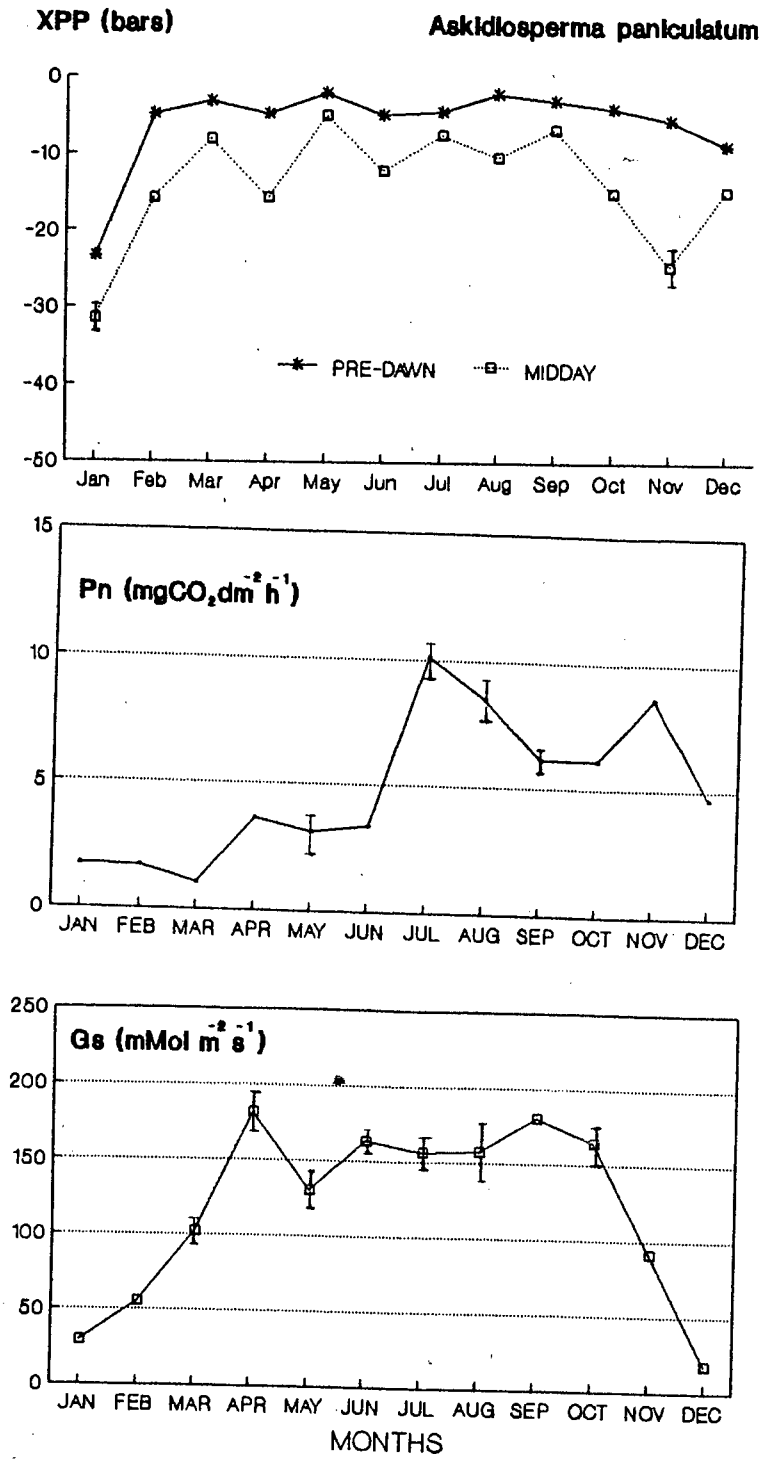


Fig.4.13: Seasonal course of xylem pressure potential (xpp), midday net photosynthetic rate (Pn) and midday stomatal conductance (Gs) of Askidiosperma paniculatum from January to December 1986.

the photosynthetic gas exchange processes (Helmuth, 1968; Oechel et al., 1972; Mooney & Chu, 1974; Odening & Strain, 1974).

In the case of T.lucens, it appears as if Pn was more strongly correlated with xpp than in the case of the ericoid plants. This is exemplified in the data obtained during April and June when unexpectedly low midday xylem pressure potentials (fig. 4.12) were experienced. The decreases in midday xpp were accompanied by similar decreases in midday net photosynthetic rate. E.plukenetii and E.hispidula also experienced similar decreases in xpp during April and June (figs. 4.9 & 4.10) but these were not accompanied by reductions in midday Pn.

While such casual observations of the data suggest that the seasonal patterns of net photosynthetic rate of T.lucens can be explained in terms of its water relations, statistical studies however, do not provide a similar picture. Regression analysis (Statgraghics, 1986) of Pn on xpp, with the latter being the independent variable, showed no statistically significant correlation between these two variables (Appendix Table 1). The antagonistic conclusions reached from observational and statistical analyses of the data stems from the shortcomings of using only field observations to determine causes and effects of certain physiological phenomena. Field observations record the

photosynthetic response to numerous factors, including that of xpp. Controlled environment laboratory experiments are needed to elucidate how strongly xpp affects Pn of the fynbos species, if it does at all.

The R-values found for the correlation between xpp and Gs, and between xpp and Pn for the two species differed widely for the two restioid species (Appendix Table 1). In contrast to the results for T.lucens, no statistically acceptable correlations between these variables were found for A.paniculatum. This suggests that these two species have different stomatal and photosynthetic responses to changes in plant water status. The contrasts between the gas exchange properties of the two restioid species studied are discussed at a later stage.

The Pn and xpp depressions experienced during April and June by T.lucens (fig.4.12) were not associated with decreases in Gs. The observed decreases in Pn were therefore possibly the result of factors other than stomatal restriction of photosynthetic C-fixation. One such possibility is the effect of low tissue water levels on biochemical properties of the photosynthetic apparatus. Helmuth (1969) also found little stomatal regulation of net photosynthesis for the Australian shrub Acacia craspedocarpa under extreme water stress. The author attributed regulation of Pn to other factors like the effects of water

status on photosynthetic biochemical processes. This was also evident from studies where net photosynthesis was depressed under water stress even though stomata were open (Boyer & Bowen, 1970). The close correlation between Pn and xpp observed for T.lucens was not evident for A.paniculatum during April and June.

The apparent lack of correlation between Gs and Pn observed for T.lucens does not imply that photosynthetic C-fixation was always accomplished independently of stomatal regulation. The diurnal patterns of photosynthetic gas exchange of T.lucens and A.paniculatum (figs 4.20 & 4.21) indicate that the variation in Gs throughout the day frequently resembled the diurnal Pn pattern, suggesting that rates of CO_2 uptake could have been strongly affected by stomatal movements. It is also noteworthy that the close association between Gs and Pn patterns only occurred during periods when plant water levels were relatively high, which in turn suggests that such a correlation is possibly only valid when water stress is not experienced.

In contrast to the ericoid species, the seasonal variation in Pn of T.lucens did not exhibit a similar well defined seasonal pattern. The midday and late-afternoon observations in particular, manifested a relatively high degree of fluctuation after summer. The possible causes for the high degree of variation in Pn of T.lucens are manifold. Firstly, the period

between sampling date and the day of last rains was not constant, and consequently the levels of soil moisture content at the 10 - 15 cm depth varied at the time when measurements were performed. Although this variation in soil water content may not always have been reflected in the xpp values, it could be associated with the fluctuations in Pn experienced by T.lucens. Morrow & Mooney (1974) indeed found a strong positive correlation between maximum rates of gas exchange and soil moisture availability and no correlation between Pn and minimum xpp.

Another possible cause for the observed higher fluctuation in Pn during periods when plant individuals experienced less water stress (less negative xpp's) is related to different adaptive strategies to cope with occasional low soil water availability. The ericoid species reduce transpirational water loss by having their stomata confined almost entirely to the non-photosynthetic grooves on the abaxial leaf surfaces. This adaptation can be considered as a dessication avoiding strategy. Anatomical investigation of T.lucens on the other hand confirmed the presence of protective cells (lignified palisade cells) described by Cutler (1969). These protective cells in addition to well defined sclerenchyma and chlorenchyma tissues could be considered as adaptations which allow T.lucens to resist dessication. The concepts of drought avoidance and resistance are in agreement with the observed relationships between Gs and Pn of T.lucens and

ericoid species. Photosynthetic activity of the ericoid species was more closely determined by Gs (fig.4.18), providing evidence that photosynthetic C-fixation was at the cost of stomatal restriction to avoid water loss. Net photosynthetic rates of T.lucens (fig.4.20) appear to be not so greatly dependent on stomatal conductance, suggesting that photosynthetic activity of T.lucens was more responsive to diurnal changes in atmospheric environmental factors (like temperature and humidity) than the photosynthetic activity of the ericoid plants. Because of the anatomical adaptations to tolerate low plant water levels, T.lucens would photosynthesize at maximum rates "allowed" by environmental factors.

Although T.lucens and Askidiosperma paniculatum are both from the restioid growth form, marked differences were observed in the seasonal patterns and in the diurnal variation of net photosyntetic rates. During summer, Pn's recorded for A.paniculatum (fig.4.13) were always higher than that of T.lucens (fig.4.12). During periods when plants presumably do not experience water stress, the net photosynthetic rates of T.lucens were sometimes higher than that of A.paniculatum. Furthermore, T.lucens showed a greater degree of seasonal variation in Pn than A.paniculatum. The diurnal Pn rates of T.lucens were also less constant and showed greater degrees of variation over the course of a single day (Fig.4.20). On the basis of the greater

frequency of major diurnal changes in Pn of T.lucens it is tempting to suggest that this species was photosynthetically more responsive than A.paniculatum to diurnal changes in the environmental factors, like temperature or humidity.

Although the differences in the diurnal and seasonal Pn patterns of T.lucens and A.paniculatum could not be accurately explained, it was established that the root:shoot ratios of these species varied and that the rooting systems of A.paniculatum penetrated deeper soil layers. These morphological characteristics could possibly be related to the observed differences in seasonal and diurnal Pn patterns.

Since periods of water stress in the fynbos biome are largely accompanied by above-average temperatures, the effect of temperature on stomatal response cannot be ignored. Acclimation of Gs to temperature can be induced in controlled environments (Neilson & Jarvis, 1975) and can also possibly occur in the field. As opposed to more arid ecosystems, the temperatures encountered in the fynbos during winter (section 3.1) are often similar to temperatures experienced during summer. The resulting broad range of temperatures during winter most likely affected the stomatal movements of the two restioid species in different ways resulting in dissimilar responses during the wetter months. Comparative interpretation of the seasonal

variation in Gs of the restioid species is difficult since there is presently no information available concerning which processes and factors affect stomatal behaviour in the various fynbos species.

Furthermore, the seasonal variation in stomatal conductance cannot easily be explained on the basis of seasonal progression in plant water status since the Gs of many species is sensitive to leaf water status over a wide but variable range (e.g. Lopushinsky, 1969). The sensitivity of stomata of some species also changes with varying levels of plant water content (Schulze et al., 1975).

4.2.3 PROTEOID SPECIES

The maximum net photosynthetic rate recorded for the juvenile and mature individuals of Protea laurifolia (figs.4.14 & 4.15) and for Leucadendron salignum (fig.4.16) were often more than twice the rates recorded for the restioid species. The seasonal Pn patterns of P.laurifolia showed largely the same features of the patterns of the ericoid and the restioid species: the lowest net photosynthetic rates were recorded during the summer months and the highest rates during the winter-spring period. The degree of summer depression in Pn for the proteoid species, however, was not nearly as large as the summer Pn depression experienced by the restioid and the ericoid species. As a percentage of the September midday Pn, the midday Pn during January was 62% and 40% for the juvenile and the mature individuals of P.laurifolia respectively. The midday Pn of T.lucens during January was 3% of the September midday Pn and that of E.plukenetii only 6%. These marked differences in the degree of summer depression in Pn between the various growth forms confirm the general picture obtained from studies on other mediterranean evergreen sclerophylls. Depth of rooting is frequently used to explain the degree of summer decline in Pn. Chaparral species with deep and extensive rooting systems, for example were found to be less sensitive (than the shallow-rooted species) to "summer drought" and could therefore maintain positive net assimilation throughout

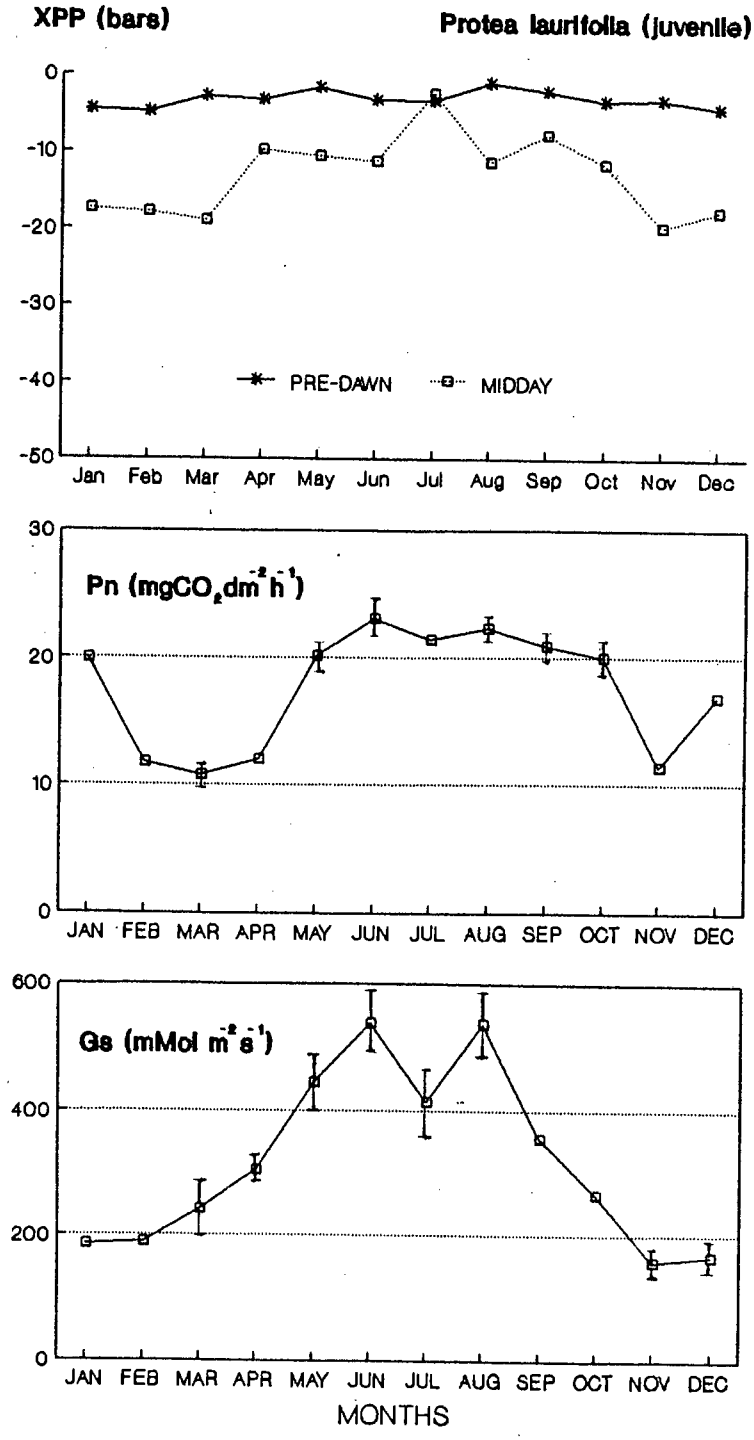


Fig.4.14: Seasonal course of xylem pressure potential (xpp), midday net photosynthetic rate (Pn) and midday stomatal conductance (Gs) of Protea laurifolia (juvenile) from January to December 1986.

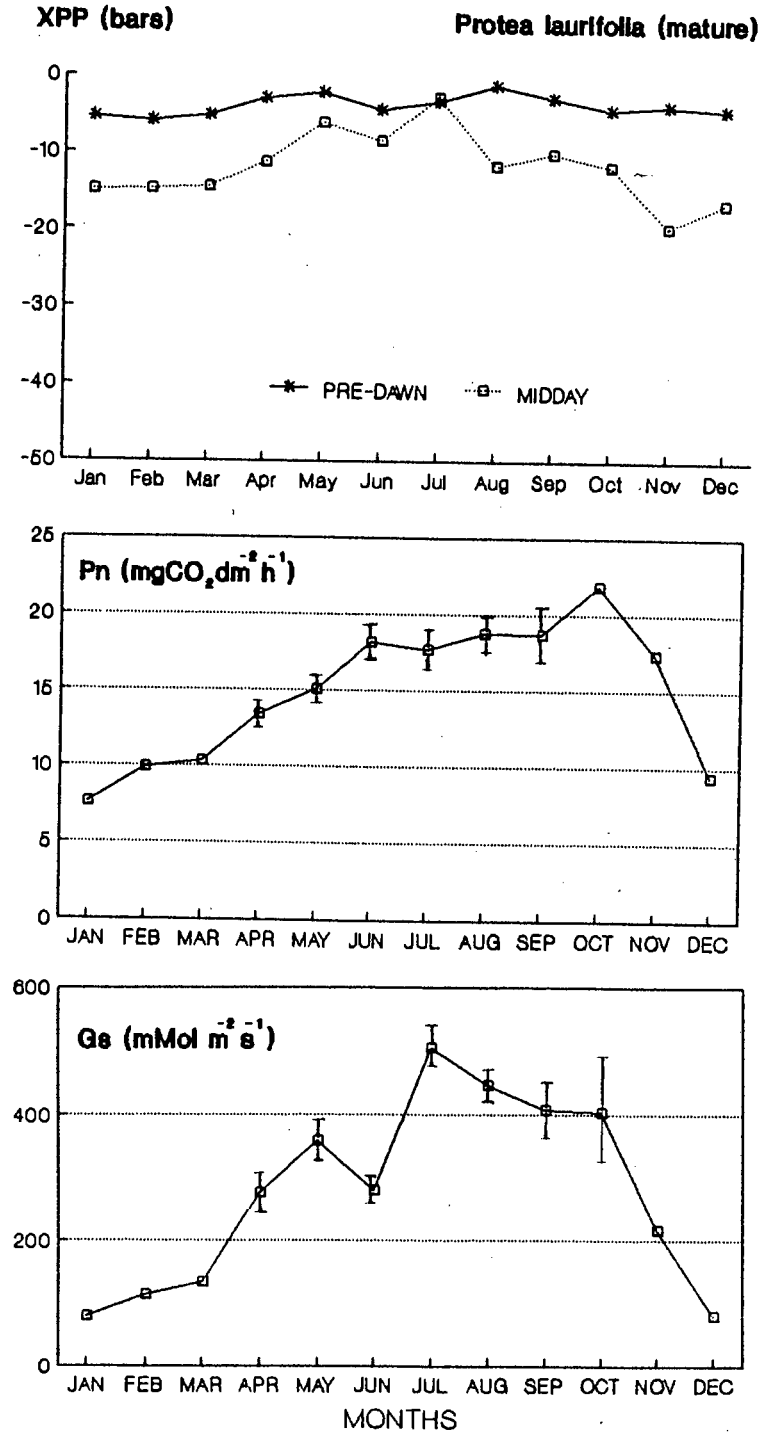


Fig.4.15: Seasonal course of xylem pressure potential (xpp), midday net photosynthetic rate (Pn) and midday stomatal conductance (Gs) of Protea laurifolia (mature) from January to December 1986.

this period (Harrison et al., 1971). Although the mature individuals maintained higher plant water status levels throughout the summer period they experienced a greater decline in Pn. This places some uncertainty on the role that water shortage could have played in limiting photosynthetic C-fixation during summer.

The seasonal changes in net photosynthetic rate of the other proteoid species, Leucadendron salignum (fig.4.16) were distinctly different from those obtained for P.laurifolia. L.salignum did not experience the severe summer depression in Pn. The highest Pn recorded for all the fynbos species studied (29.3 $mgCO_2$ dm^{-2} h^{-1}) was recorded for L.salignum during December (fig.4.24).

There is no experimental evidence to account for the difference in extent of summer depressions observed between the proteoid species. Regression analysis has shown that photosynthetic rates of the proteoid species do not correlate with their xxp's (Appendix Table 1). It therefore cannot easily be assumed that the lower Pn's observed during summer were in response to reduced (more negative) xpp's measured during this period. L.salignum

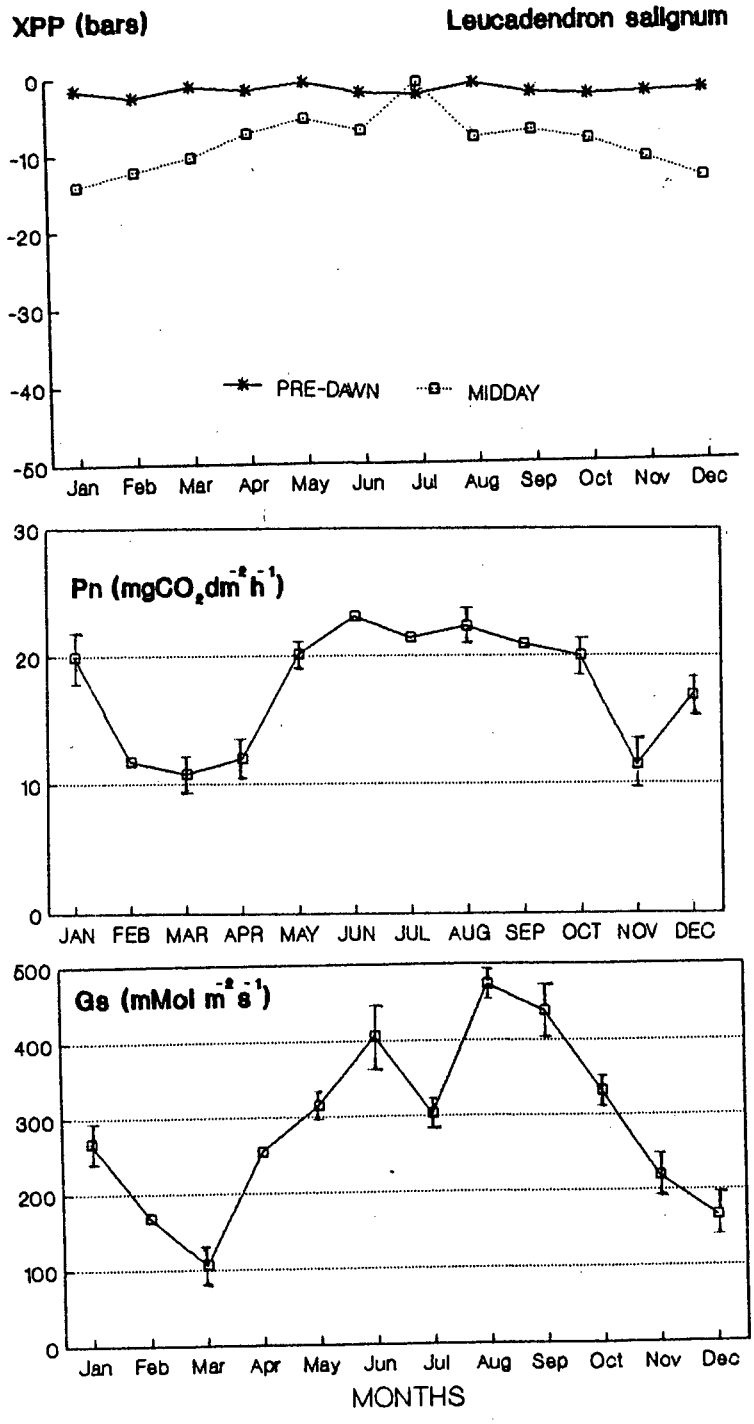


Fig.4.16: Seasonal course of xylem pressure potential (xpp), midday net photosynthetic rate (Pn) and midday stomatal conductance (Gs) of Leucadendron salignum from January to December 1986.

must be photosynthetically less sensitive to some stress factor (other than low tissue water status) experienced during summer. When the higher temperatures generally encountered during summer (fig.3.10) are considered as a possible stress factor, then it appears as if L.salignum is better suited to maintain more constant Pn's throughout the year. L.salignum with approximately one-tenth the leaf size of P.laurifolia was probably able to maintain lower leaf temperatures, thereby reducing the possible deleterious effects of high temperatures on leaf photosynthetic processes.

The net photosynthetic rate of P.laurifolia seedlings (Fig.4.25) differed from those recorded for the mature individuals (fig.4.26). For the juveniles, the maximum Pn was recorded during June (mean value of 27.6 $mgCO_2\ dm^{-2}\ h^{-1}$) while the maximum of the mature ones (21.8 $mgCO_2\ dm^{-2}\ h^{-1}$) was recorded during October. As was indicated earlier, the rate of decline in Pn from the maximum (winter-spring) to the minimum during summer differed. When the January midday Pn is expressed as a percentage of the September midday Pn, the mature plants experienced a 60% summer depression in Pn while the juveniles experienced a decrease of 38%.

The greater summer decline in Pn and the more pronounced midday depression in Pn of the mature individuals of P.laurifolia

suggest that some limiting factor during summer had a greater influence on the mature plants than on the seedlings. The limiting factor could not be related to a water shortage since the mature plants were able to maintain higher midday xpp values (less negative) throughout the summer (section 4.1). However, it could also be argued that the seedlings had a different threshold xpp at which Pn was impaired.

It is also likely that the decline in net photosynthetic rate, and the decrease in efficiency of CO_2 fixation during summer, with increasing plant age of P.laurifolia could be due to the decrease in foliage nutrient concentrations. Before further inferences can be made, however, a much more detailed knowledge of nutrient pools in the different ages of plant individuals is necessary. It is further necessary to know how low levels of certain nutrients could limit photosynthetic C-fixation in the fynbos.

Furthermore, the leaf density and the branched nature of the mature plants possibly created different microclimates where relative humidities were higher and temperatures possibly lower. How these environmental factors affect net photosynthesis in the different aged P.laurifolia individuals still needs to be investigated.

The measured stomatal conductances of P.laurifolia (figs.4.28 & 4.29) were almost always twice the values recorded for the restioid species (figs.4.19 & 4.20). These observations correlate well with the Pn data since the net photosynthetic rates of the proteoid species (figs.4.25 & 4.26) were also frequently twice the rates recorded for the restioid species (figs.4.17 & 4.18).

Generally, there appears to be a good relationship between Gs and Pn of P.laurifolia: the increased Gs values recorded from April to October were accompanied by elevated net photosynthetic rates. It has already been stated earlier that increased stomatal conductance does not necessarily imply increased rates of photosynthetic C-fixation, particularly during stress periods. Non-stomatal responses to stress factors might then be more important in determing Pn. This was particularly well illustrated for L.salignum (fig.4.24) where the maximum Pn recorded during December was not accompanied by the maximum Gs (fig.4.23).

4.2.4 METROSIDEROS ANGUSTIFOLIA

The net photosynthetic rates recorded for M.angustifolia (fig.4.17) were of the same order as the Pn values recorded for the proteoid species. The seasonal Pn patterns had characteristics common to both P.laurifolia and L.saligna. There were indications of summer depression in Pn, but to a lesser extent than the summer depression observed for P.laurifolia (figs.4.14 & 4.15). If the rates obtained for M.angustifolia for the three different times of the day are averaged, the resultant mean daily Pn values for the autumn and for the spring months are the highest, which is similar to the seasonal Pn patterns of L.salignum (fig.4.16). The riparian habitat (growth along streambanks) of M.angustifolia permitted a continuous supply of soil water which could have the same adaptive advantage as the resprouting nature of L.salignum. However, it is not yet proved that the water factor is of overriding importance in determining rates of photosynthesis in these species. Regression analyses (Statgraph,1986) indeed showed no significant statistical correlations between Pn and xpp, and between Gs and xpp (Appendix Table 1). It is unlikely that photosynthetic rates of M.angustifolia were limited by water shortage during summer since the summer xpp's were at the most only 6 bars less than the xpp's recorded during spring. The lack of experimental data on stomatal and photosynthetic responses to environmental

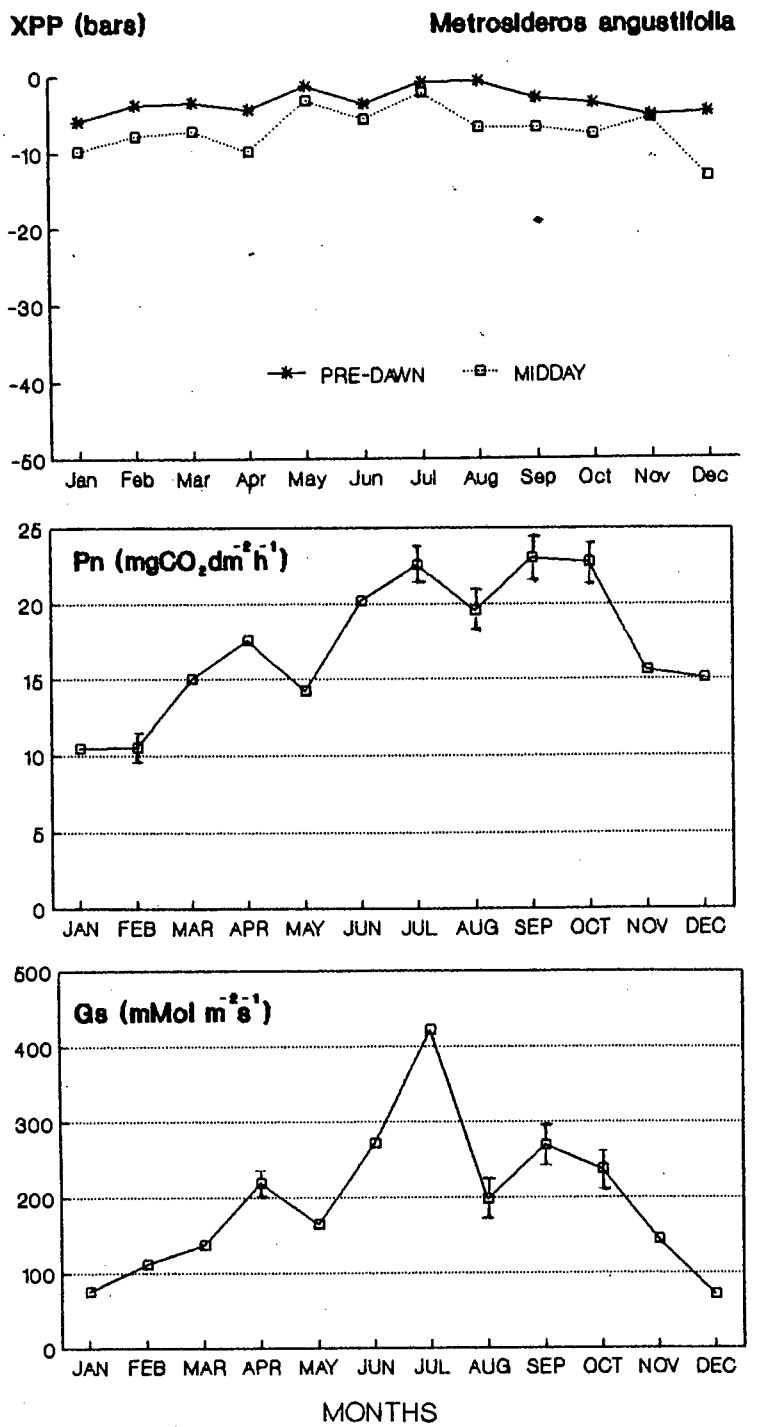


Fig.4.17: Seasonal course of xylem pressure potential (xpp), midday net photosynthetic rate (Pn) and midday stomatal conductance (Gs) of Metrosideros angustifolia from January to December 1986.

factors prevents a thorough understanding of the relative importance of water shortage and temperature in determining photosynthetic activity during summer.

The seasonal pattern of stomatal conductances recorded for M.angustifolia (fig.4.17) are comparable to the Gs patterns recorded for P.laurifolia (figs.4.14 & 4.15), i.e. reduced stomatal conductance experienced during summer months. The marked diurnal changes in Gs observed from February to December (fig.4.25) further suggests that stomatal activity was quite sensitive to diurnal changes in atmospheric environmental factors. The Gs values were always lower than the values recorded for the proteoid species and this can be related to the stomata being found only on the abaxial leaf surfaces.

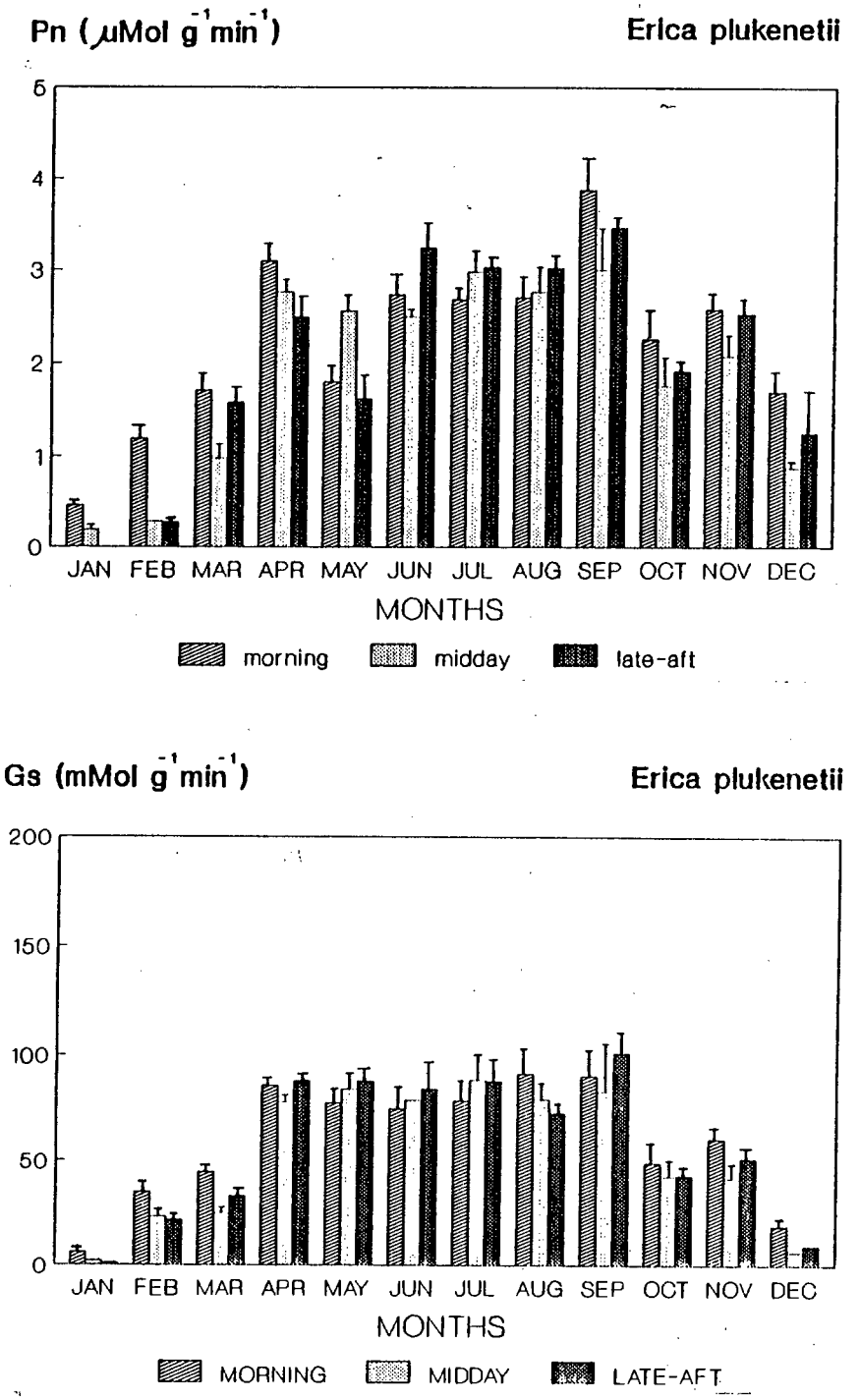
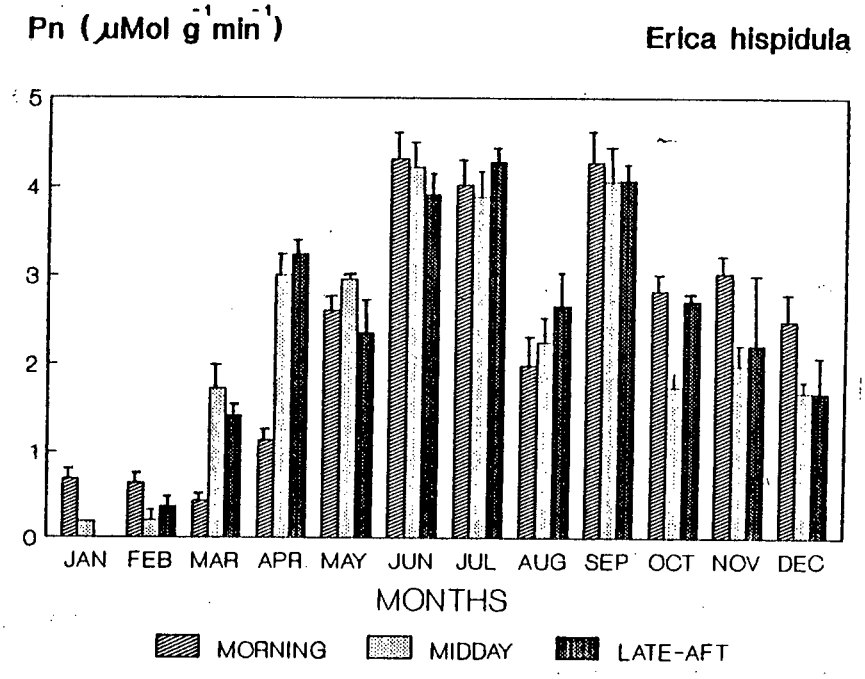


Fig.4.18: Seasonal course of diurnal variation in net photosynthetic rate (Pn) and stomatal conductance (Gs) of Erica plukenetii.



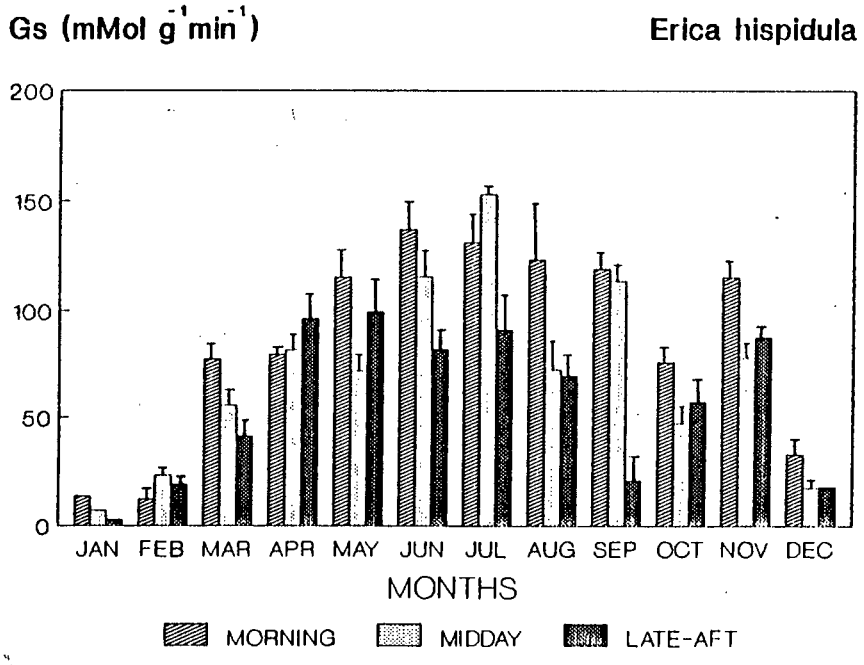


Fig.4.19: Seasonal course of diurnal variation in net photosynthetic rate (Pn) and stomatal conductance (Gs) of Erica hispidula.

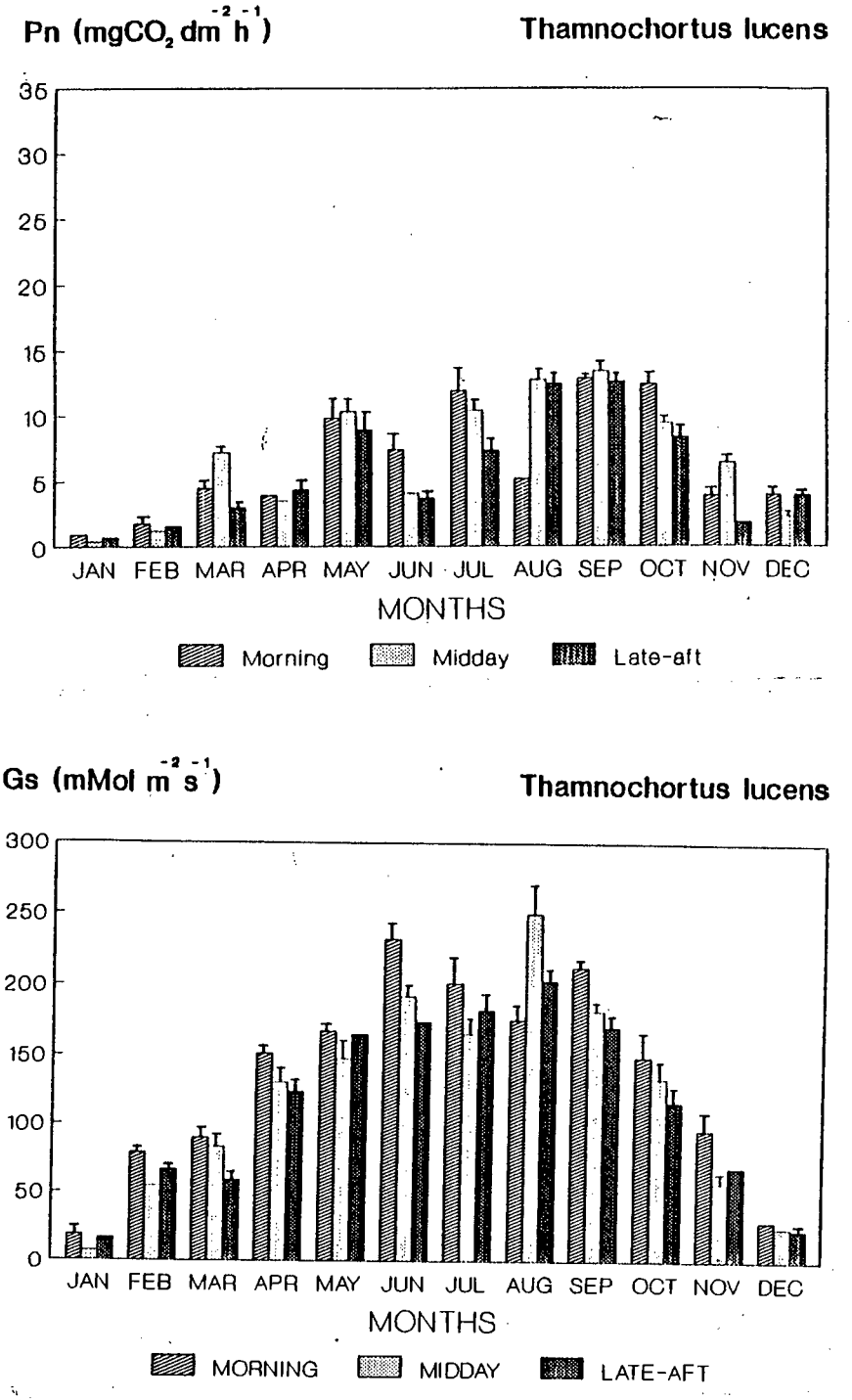
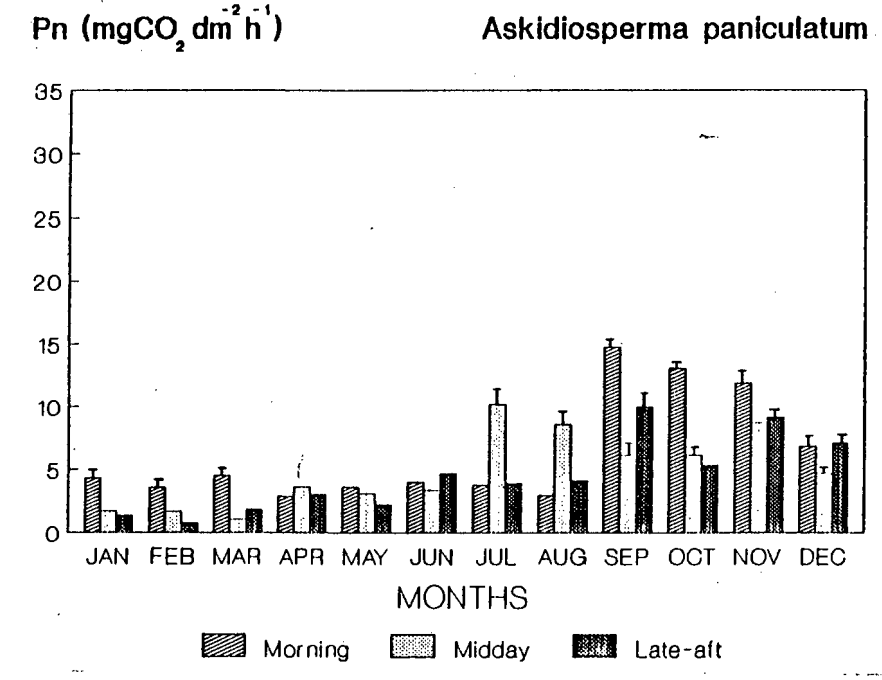


Fig.4.20: Seasonal course of diurnal variation in net photosynthetic rate (Pn) and stomatal conductance (Gs) of Thamnochortus lucens.



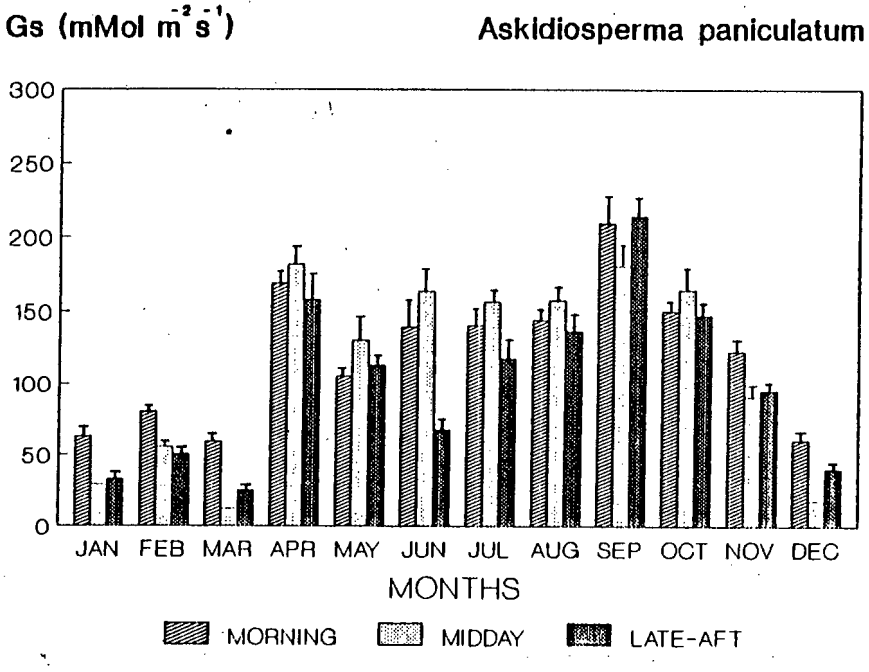
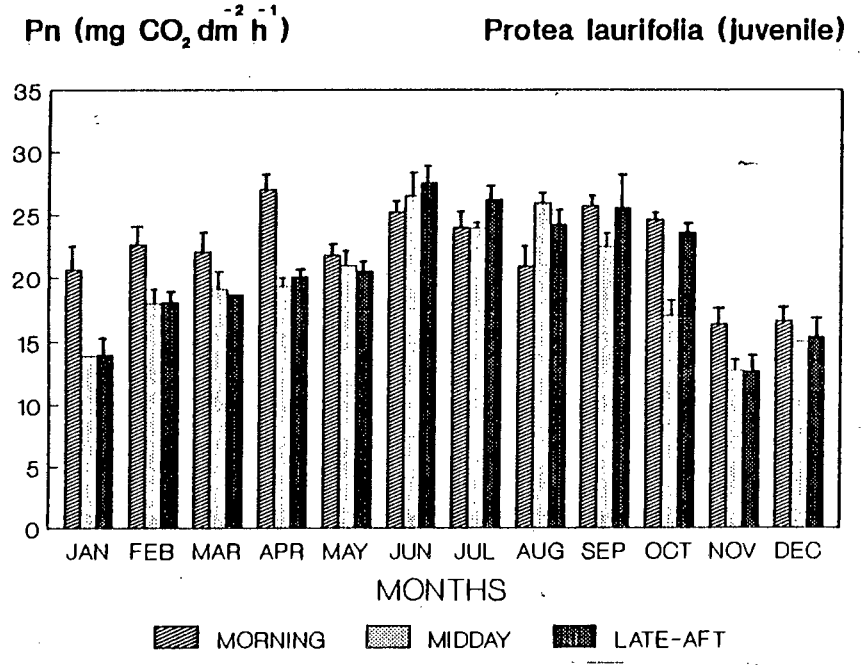


Fig.4.21: Seasonal course of diurnal variation in net photosynthetic rate (Pn) and stomatal conductance (Gs) of Askidiosperma paniculatum.



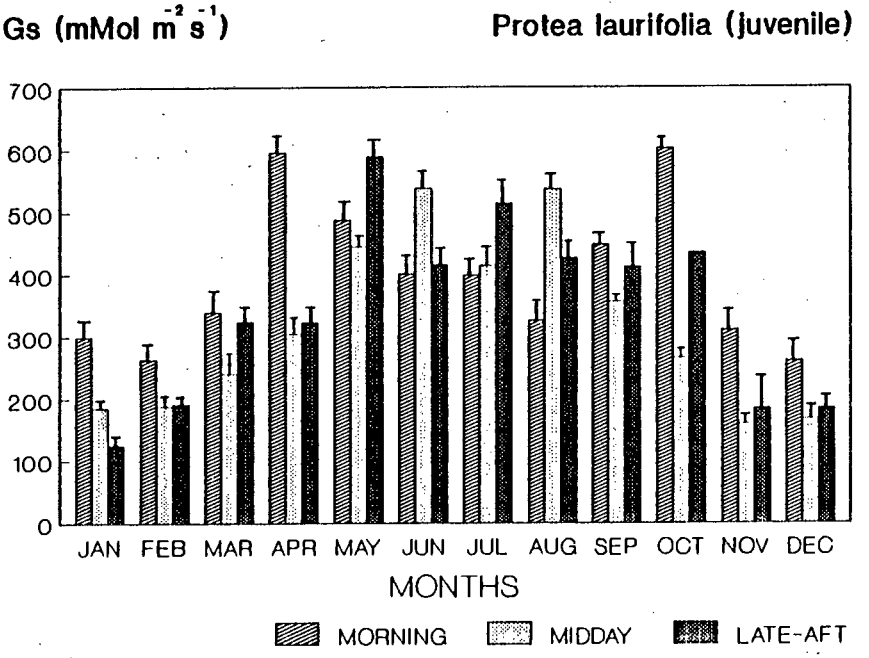
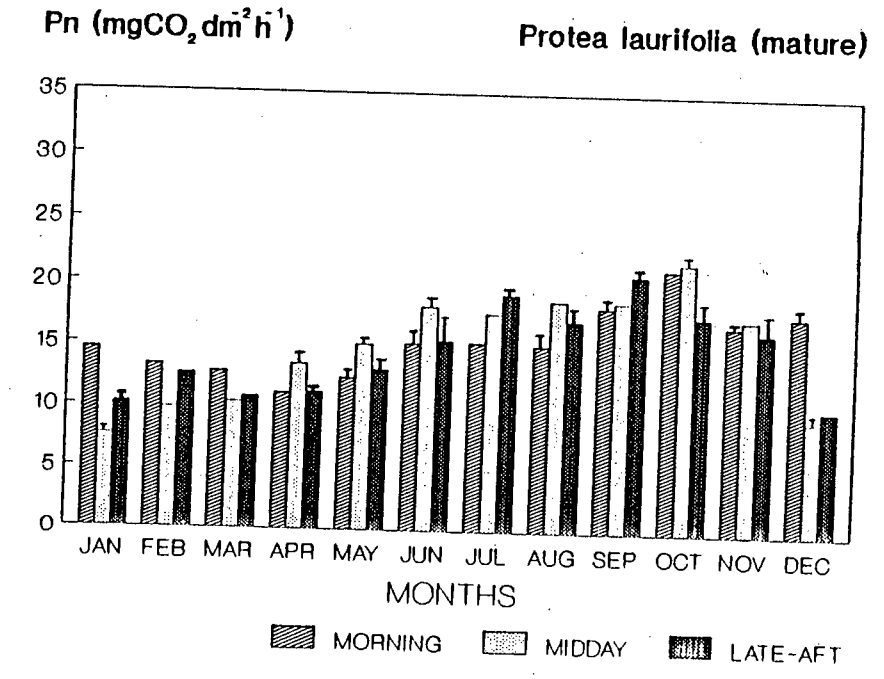


Fig.4.22: Seasonal course of diurnal variation in net photosynthetic rate (Pn) and stomatal conductance (Gs) of Protea laurifolia (juvenile).



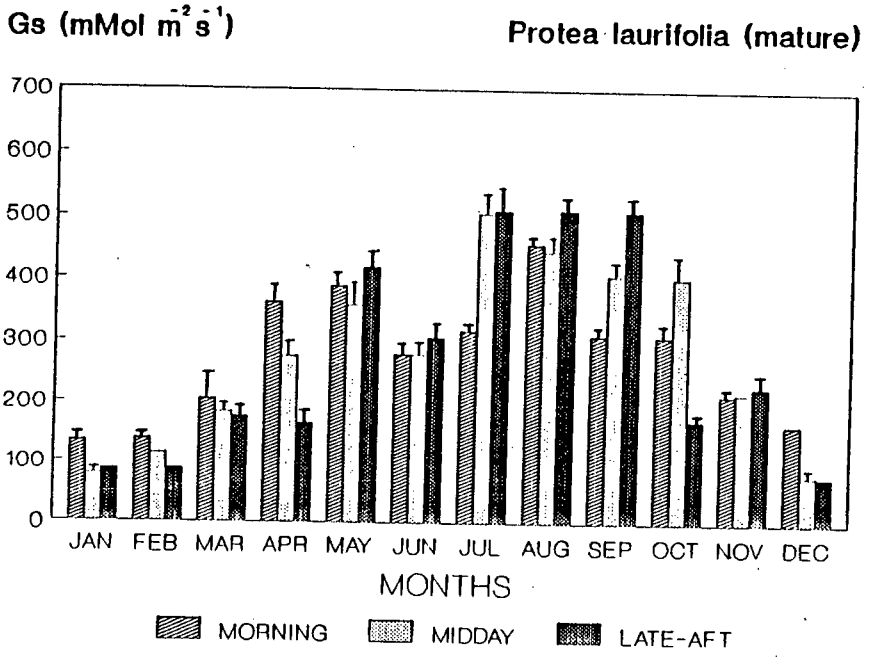
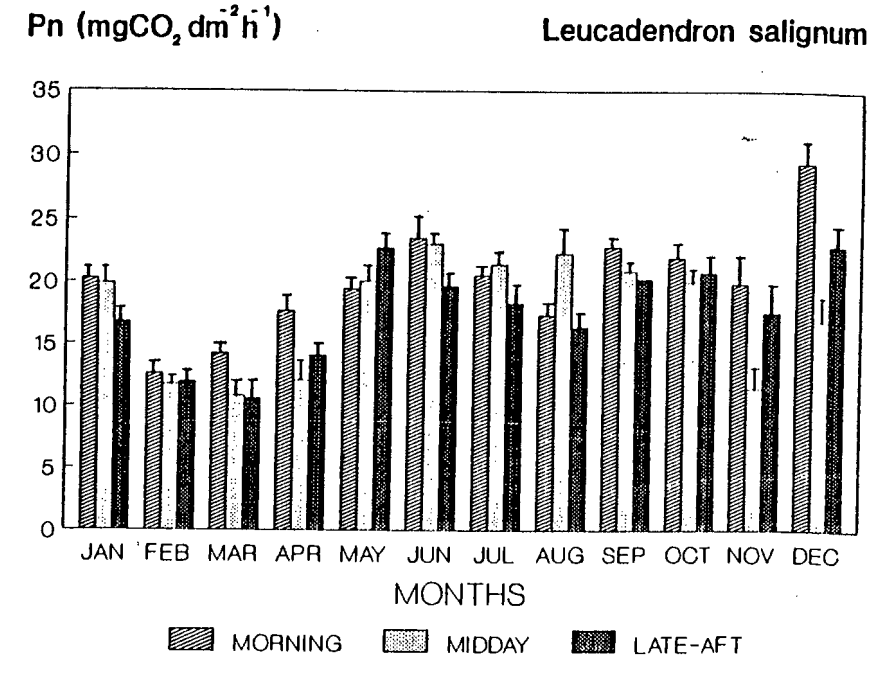


Fig.4.23: Seasonal course of diurnal variation in net photosynthetic rate (Pn) and stomatal conductance (Gs) of Protea laurifolia (mature).



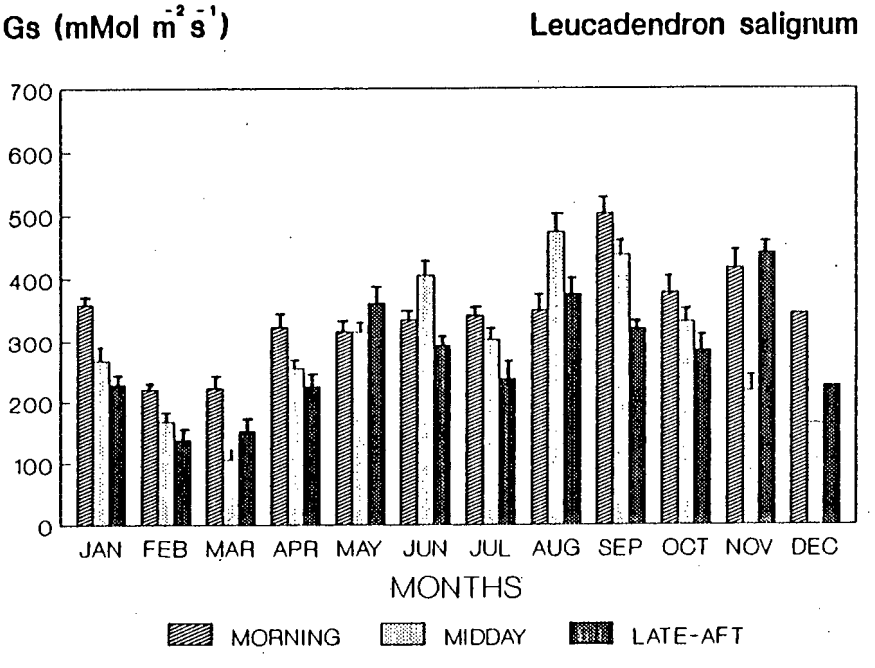


Fig.4.24: Seasonal course of diurnal variation in net photosynthetic rate (Pn) and stomatal conductance (Gs) of Leucadendron salignum.

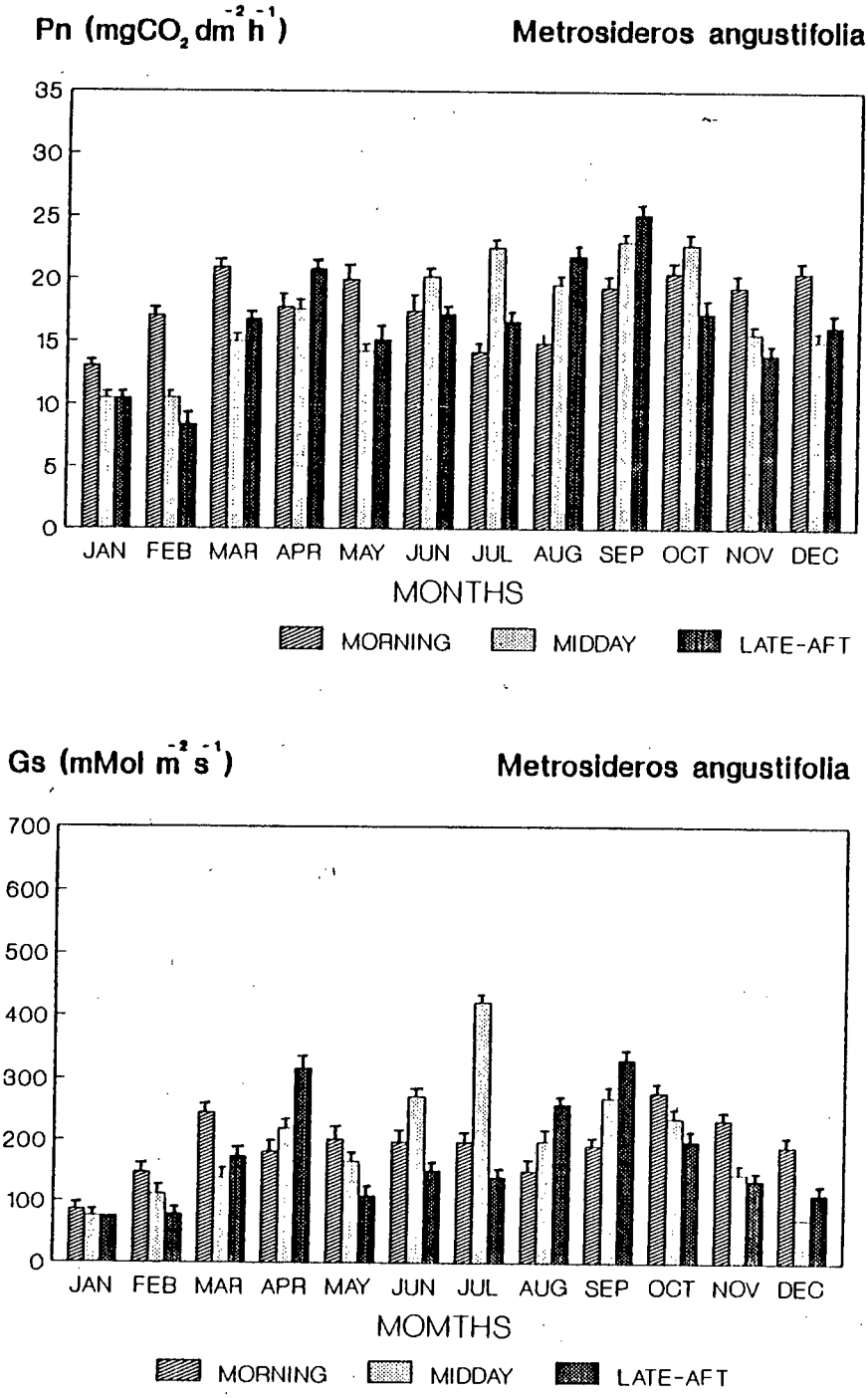


Fig.4.25: Seasonal course of diurnal variation in net photosynthetic rate (Pn) and stomatal conductance (Gs) of Metrosideros angustifolia.

4.3 SEASONAL PROGRESSION AND DIURNAL VARIATION IN TRANSPIRATION RATE

Each value in the figure series 4.26 to 4.29 is the mean of 6 replicate measurements and the corresponding vertical bar represents the standard error of the mean (SEM). The absence of a vertical bar signifies that the SEM is too small to show on the scale of the graph.

The measured transpiration rates (Tr) of the ericoid species (fig.4.26) and of the restioid species (fig.4.27) showed similar seasonal patterns: minimum values were recorded during summer. The highest Tr's were recorded during spring and autumn, possibly because soil water levels were higher and the relatively higher temperatures caused increases in evapotranspirative demands. The transpiration rates of the two restioid species were generally of the same magnitude but the rate of decline from the maximum (spring-summer) to the lowest (summer) values varied. The lowest Tr of A.paniculatum, measured during March, was 15% of the maximum measured during April. The lowest Tr of T.lucens, however, was only 6% of the maximum transpiration rate recorded during April.

Transpiration rates recorded for the seedlings and for the mature plants of P.laurifolia (fig.4.28) showed similar seasonal patterns. The lowest rates were recorded during the summmer and the winter months. The low values recorded during the summer

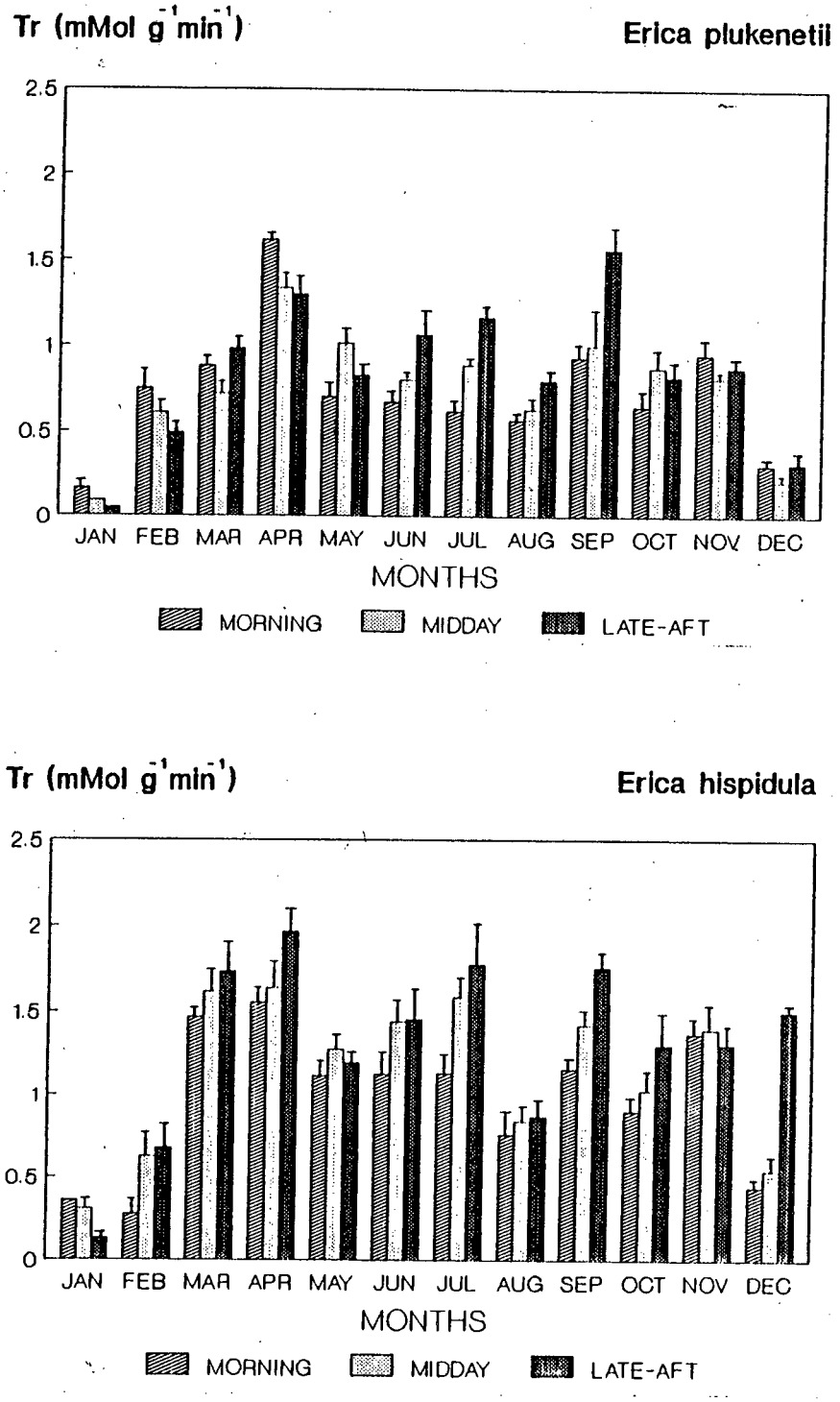
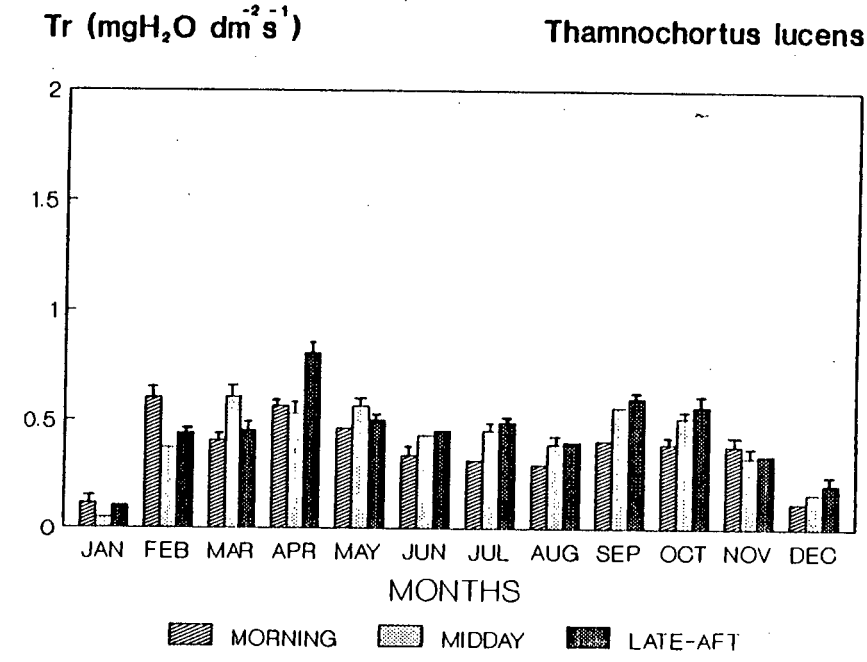


Fig.4.26: Seasonal course of diurnal variation in transpiration rates of E.plukenetii and E.hispidula.



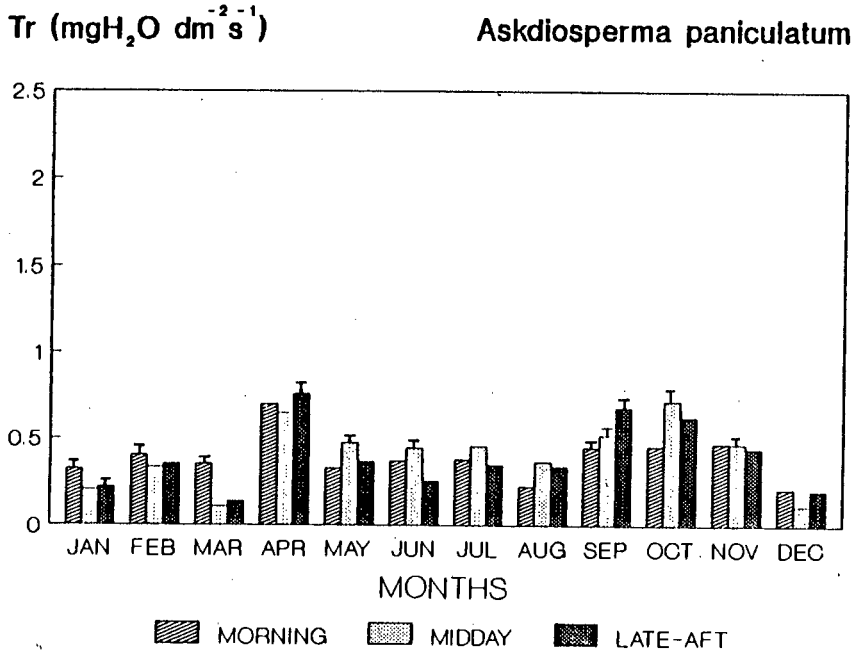


Fig.4.27: Seasonal course of diurnal variation in transpiration rates of T.lucens and A.paniculatum.

were possibly in response to decreased stomatal conductance (figs. 4.22 & 4.23). Similar to the patterns observed for the restioid and for the ericoid species, P.laurifolia (mature and juvenile) also experienced its maximum transpiration rates during autumn and spring. An adequate water supply and the concomitant higher temperatures (higher than winter) possibly contributed to the increases in transpiration rate experienced during these periods.

Comparison of the seasonal patterns of gas exchange indicates that the variability in Gs is more closely related to the variation in Pn (on a seasonal basis) than to the variation in Tr. In other words, the seasonal changes in Gs do not accurately reflect the variation in transpirational water loss, which suggests that changes in stomatal conductance are more closely associated with Pn than with Tr. The greater association of Gs with Pn was also illustrated for a number of European mediterranean species by Lange et al.(1982).

In contrast to the seasonal Tr patterns observed for P.laurifolia, the restioid and the ericoid species, L.salignum (fig.4.29) experienced its highest rates of transpiration during summer. This species could therefore be considered as being less sensitive to the generally lower soil water availablity during

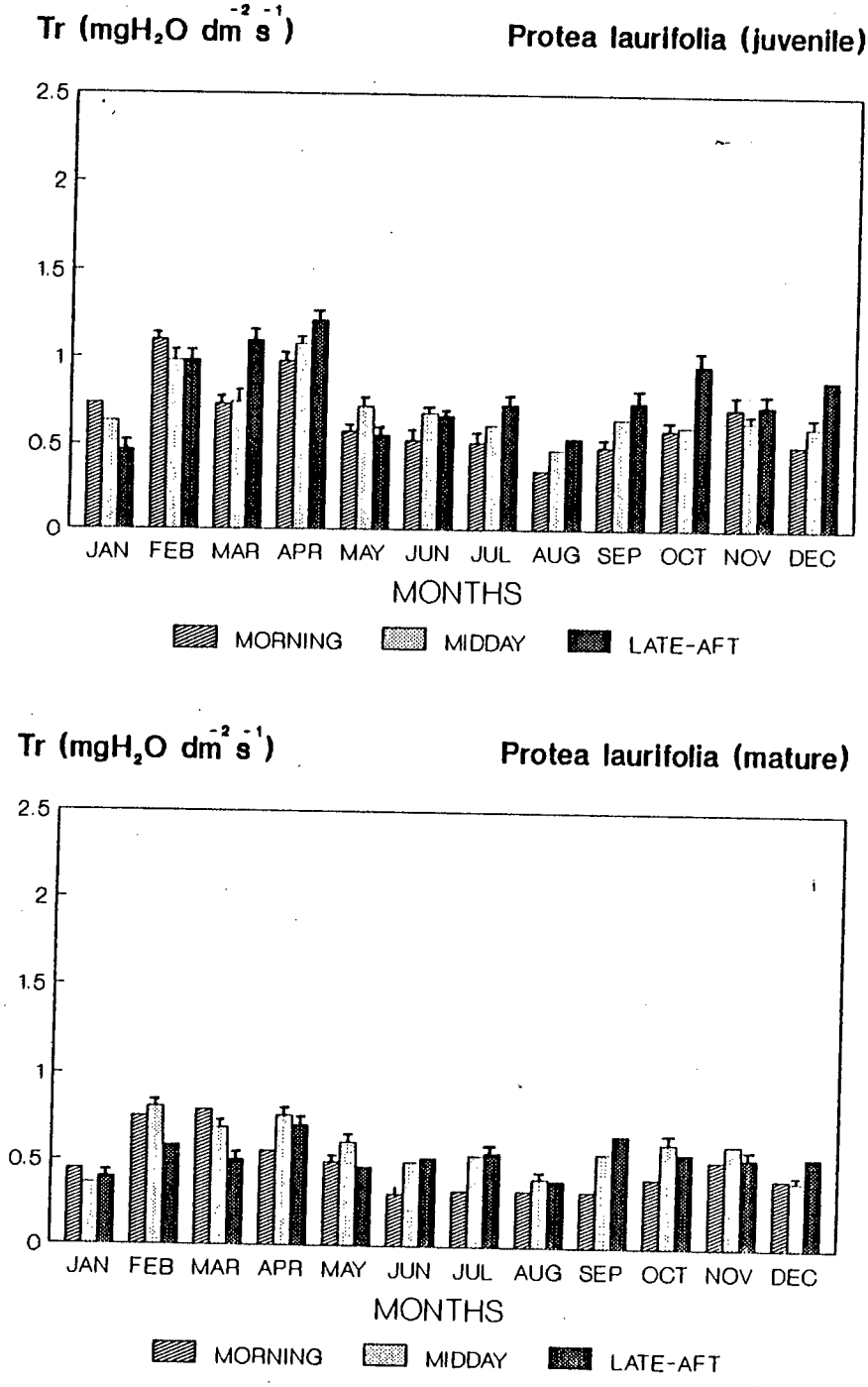


Fig.4.28: Seasonal course of diurnal variation in transpiration rates of juvenile and mature individuals of P.laurifolia.

summer. Since gas exchange measurements were performed on L.salignum individuals which resprouted after fire, these individuals had the advantage of an established rooting system which ensured an adequate supply of soil water source throughout summer. The other species studied are not resprouters and grow new roots from seed. That water was never a limiting resource for L.saligna is further illustrated by the fact that this species experienced the highest Tr's throughout the year.

The seasonal Tr patterns of M.angustifolia (fig.4.29) resemble the seasonal patterns observed for P.laurifolia (fig.4.28) in that maximum rates of transpiration were recorded during spring and autumn. That lower Tr's were recorded during summer was possibly due to stomatal control of water loss as indicated by decreases experienced in Gs during this period (fig.4.25). The low transpiration rates recorded during winter on the other hand were possibly in response to reduced evapotranspirational demands, related to lower temperatures experienced during these months.

Regression analysis (Statgraphics, 1986) of Tr and xpp (Appendix Table 1), with the latter being the independent variable, showed that for the shallow-rooted species, the observed transpiration rates were more closely associated with plant water status (xpp) than it was for the deep-rooted species. This suggests that

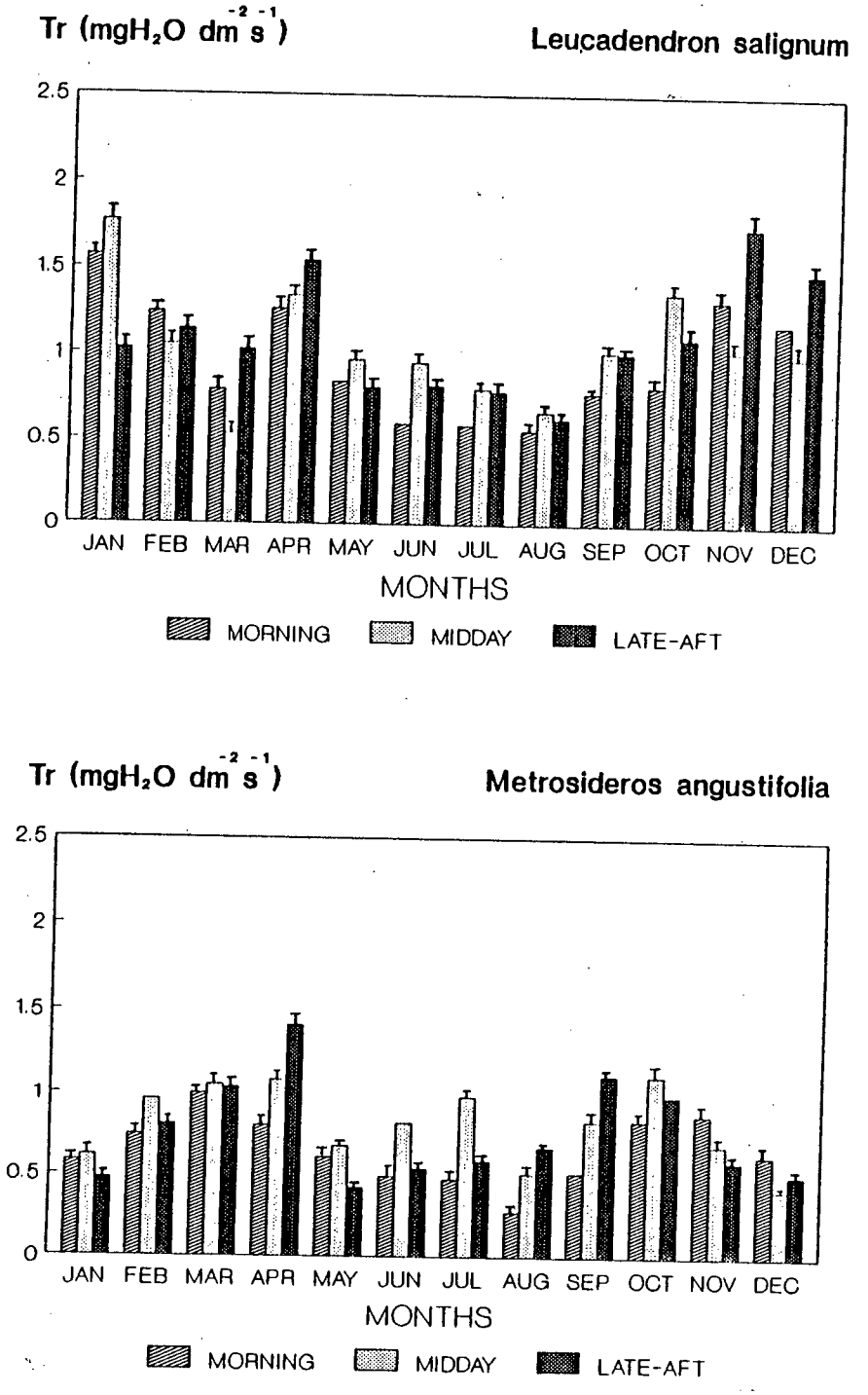


Fig.4.29: Seasonal course of diurnal variation in transpiration rates of L.salignum and M.angustifolia.

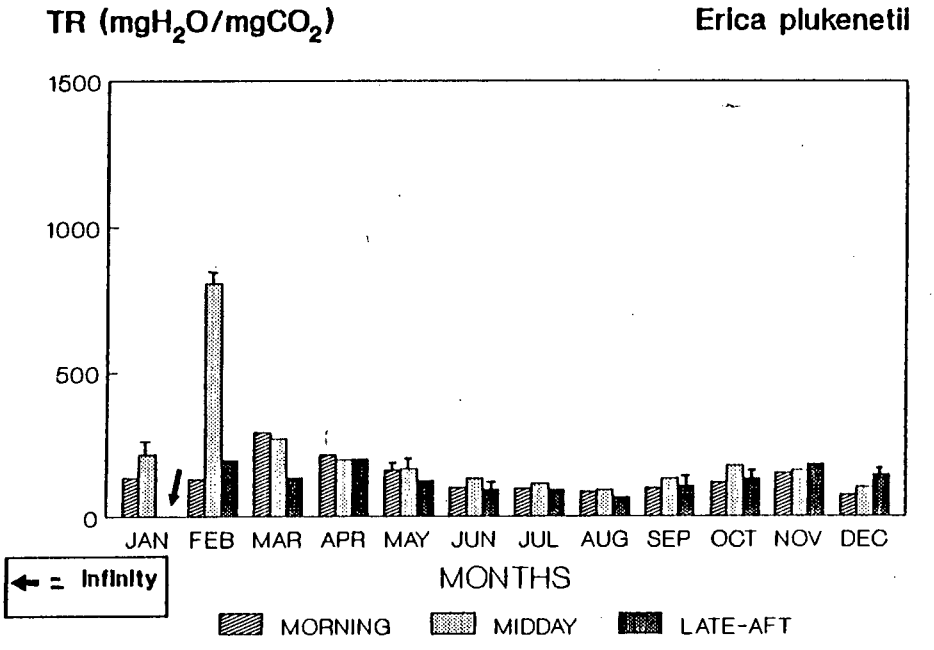
restriction of water loss is of greater importance for the shallow-rooted species. It is of interest that the correlation found between the observed Tr's and xpp's of A.paniculatum (R = 0.150) was comparable to those found for the deep-rooted species. This supports the findings, mentioned earlier, that the rates of gas exchange processes of A.paniculatum and T.lucens are possibly not determined by the same environmental factors.

4.4 EFFICIENCY OF WATER USAGE

Each value in the figure series 4.30 - 4.33 is expressed as the mean of 6 replicate measurements and the corresponding vertical bar represents the standard error of the mean (SEM). Where there are no vertical bars, the SEM is too small to show on the scale of the graph.

Transpiration ratio (TR) was calculated for E.plukenetii and E.hispidula (fig. 4.30) as the amount of water lost per unit CO_2 fixed i.e. the efficiency of water utilization in terms of C-fixation. Apart from increases in TR experienced from January to March, relatively constant transpiration ratios were maintained throughout the year. The observed increases in TR during these months were possibly a response to higher temperatures and the concomitantly greater evapotranspirative demands. In comparison to the transpiration ratios calculated for the restioid species, the ericoids were fairly economical in their water usage. The ability to maintain the lower transpiration ratios was probably related to a greater control of transpirational water loss facilitated by limited stomatal distribution on non-photosynthetic grooves on the lower leaf surfaces. The differences in absolute TR's between E.plukenetii and E.hispidula could be ascribed to the higher transpiration rates measured for E.hispidula throughout the year.

The calculated transpiration ratios (TR's) of T.lucens and of



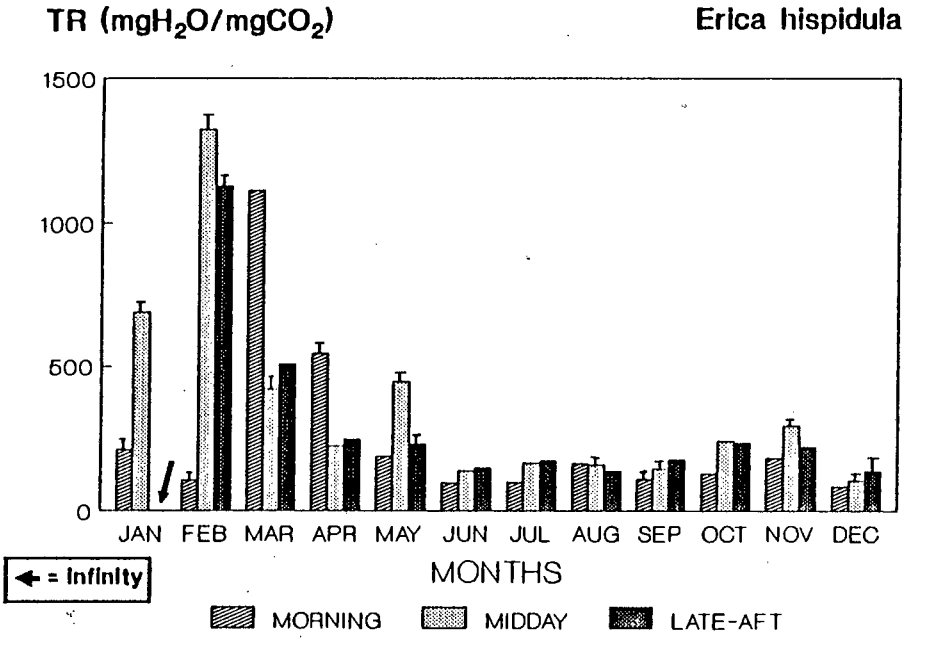


Fig.4.30: Seasonal course of diurnal variation in transpiration ratios of E.plukenetii and E.hispidula.

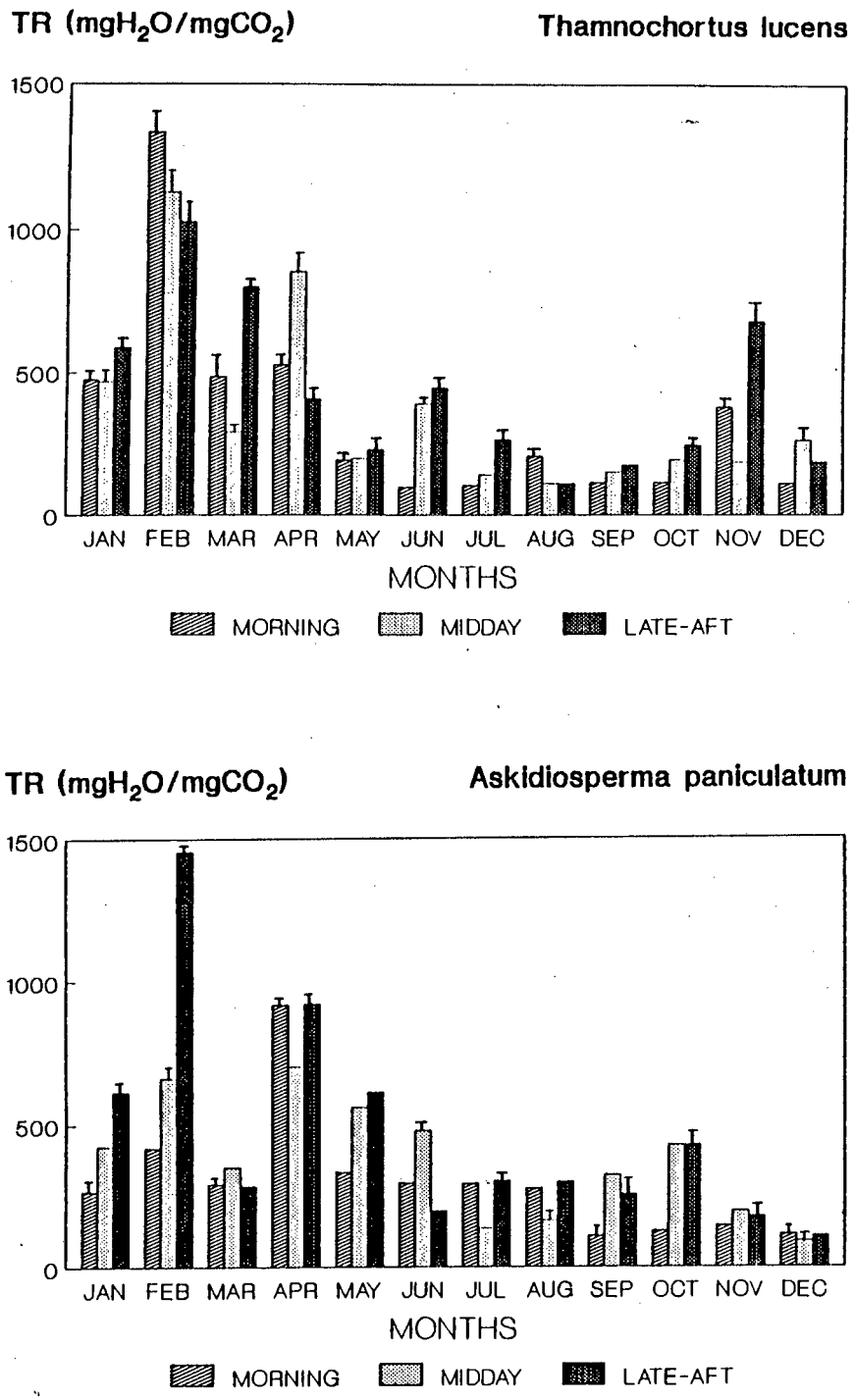


Fig.4.31: Seasonal course of diurnal variation in transpiration ratios of T.lucens and A.paniculatum.

A.paniculatum (fig.4.31) were largely of the same order. Both species were most inefficient in their water utilization with respect to C-fixation during February when low rates of net photosynthesis were accompanied by high rates of transpiration. The maximum values obtained for the restioid species were approximately twice the values recorded for E.plukenetii (fig.4.30) and generally of the same magnitude as the values recorded for E.hispidula.

Of the proteoids, the transpiration ratios (TR's) of L.salignum (fig.4.33) were the highest. The high TR values of L.salignum can be attributed to the high transpiration rates measured for this species. The TR's of L.saligum were the lowest during winter because of the decreased transpiration rates experienced during this period. The lowest TR values of P.laurifolia (fig.4.32) were also experienced during the winter months, but in this case it was possibly due to increased net photosynthetic rates. The magnitudes of the calculated TR values of the seedlings and of the mature individuals of P.laurifolia were markedly different. The seedlings lost relatively more water per unit CO_2 fixed (higher TR's) during summer in comparison to the rest of the year. Although the root:shoot ratios of the seedling may be comparable to that of the mature plants of P.laurifolia, the rooting systems of the juveniles only penetrated the first 40 cm of the soil (personal observation). The soil layers in which the roots of the seedling were confined might have experienced water deficits during summer.

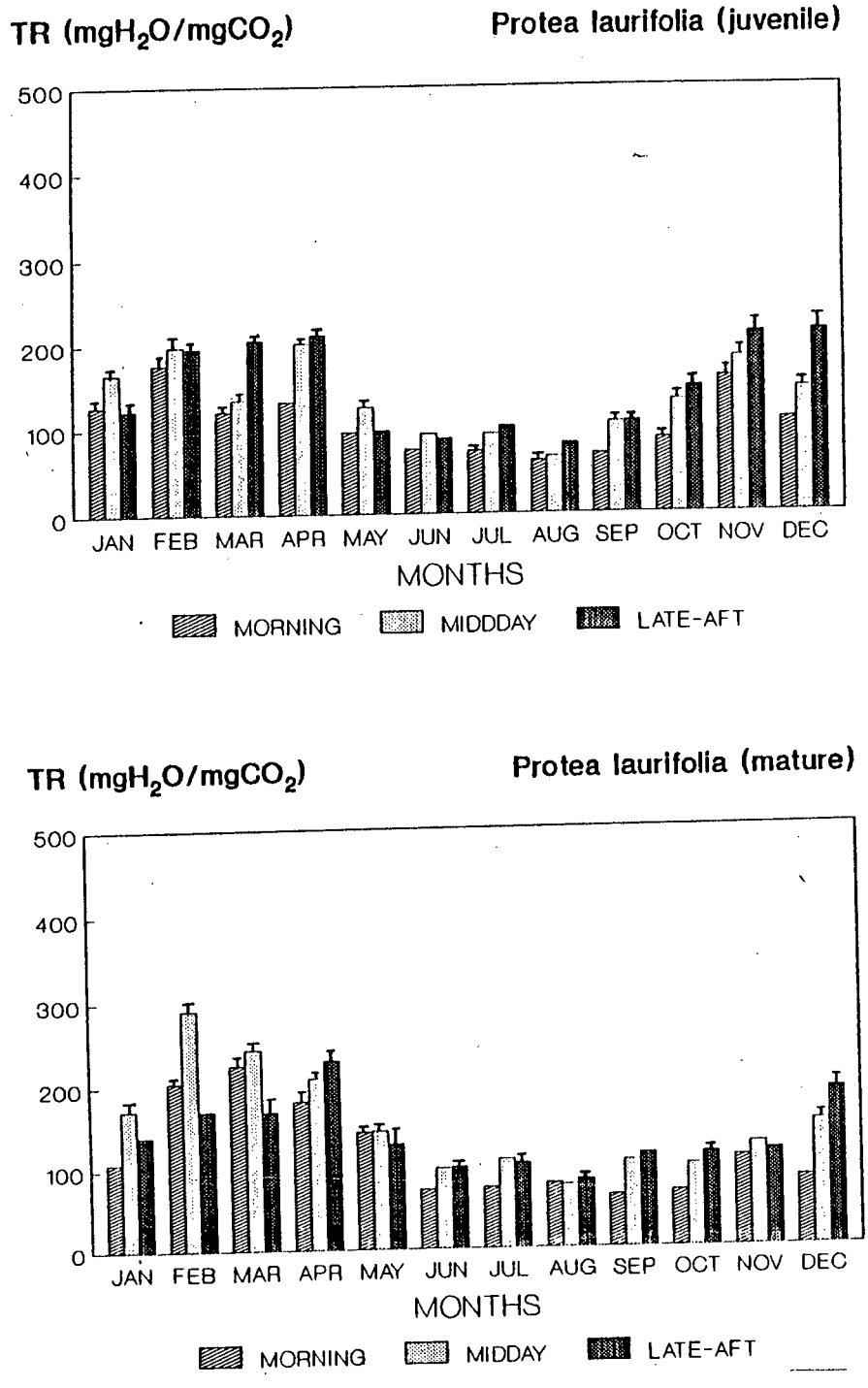


Fig.4.32: Seasonal course of diurnal variation in transpiration ratios of juvenile and mature individuals of P.laurifolia.

In comparison to the restioid species (fig.4.31), the proteoid species were relatively economical in their water usage with respect to carbon assimilation. P.laurifolia and L.salignum were able to maintain low TR's throughout the study period by virtue of their high net photosynthetic rates.

There are also indications that the proteoid species were more efficient in their water usage during the morning. This was particularly evident for the juvenile individuals of P.laurifolia (fig.4.32) for which the morning TR values were always lower than the midday values. For the mature plants of P.laurifolia (fig.4.32) and for L.salignum (fig.4.33) it was not always the case that the morning TR was lower than the midday TR. The general increase in leaf to air water vapour deficit as a result of decreasing relative humidities from the morning to midday can possibly account for this pattern. The concomitant midday decrease in stomatal conductance (not always during winter) resulted in a decline in Pn but mostly did not affect Tr, which in turn resulted in overall increases in TR during midday.

The transpiration ratios of M.angustifolia (fig.4.33) were comparable to those of the proteoid species. The high TR's calculated for February were possibly a result of the low Pn values and the high transpiration rates experienced towards the end of summer.

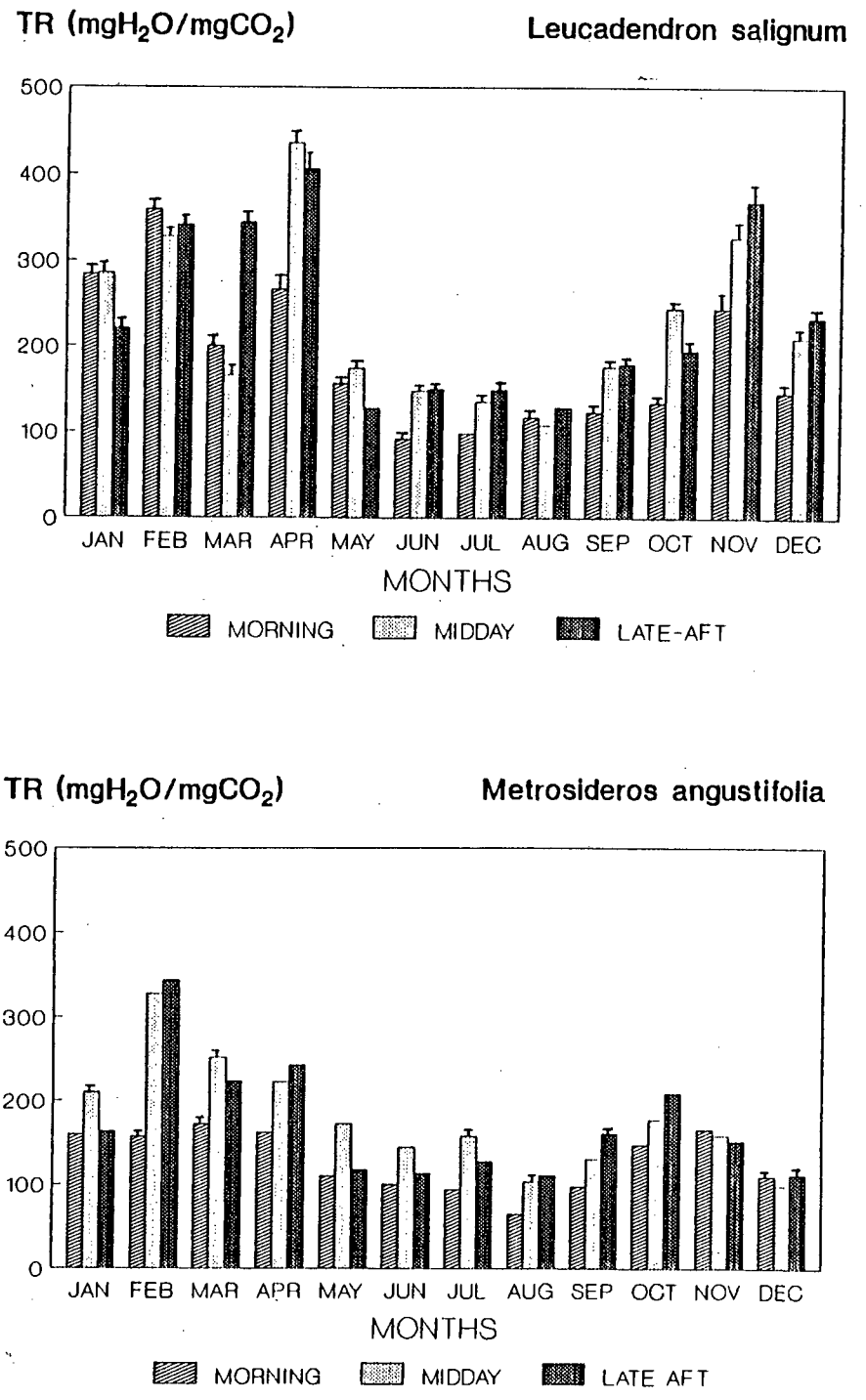


Fig.4.33: Seasonal course of diurnal variation in transpiration ratios of L.saligna and M.angustifolia.

4.3 PHOTOSYNTHETIC RESPONSE TO TEMPERATURE AND IRRADIANCE

The combined effects of irradiance and temperature on the net photosynthetic rate of Thamnochortus lucens, Protea laurifolia and Erica plukenetii were investigated experimentally in November 1986 and again in February 1987. The methods used were described in section 3.4. The results of these two sets of experiments are shown in figs. 4.41 and 4.42. Each data point on the various graphs represents an average of three measurements. The calculated standard errors were too small to show on the scale of the graphs. Maximum photosynthetic rates obtained under the experimental conditions were comparable to the rates found for the same species in a seasonal study of the diurnal variations in photosynthetic rate (refer to section 5.1).

Results obtained during February

During February, the shapes of the temperature response curves were generally similar for the three species (fig.4.42). The highest photosynthetic rates were measured at temperatures close to 20°C. The decline in photosynthesis at the extremes of temperatures was surprisingly low. At the highest temperatures in combination with the lowest light intensities, however, photosynthetic activity was often not evident (fig.4.42). Photosynthetic light saturation for Thamnochortus and Protea occurred at approximately 1000 $\mu E\ m^{-2}\ s^{-1}$. Photosynthetic

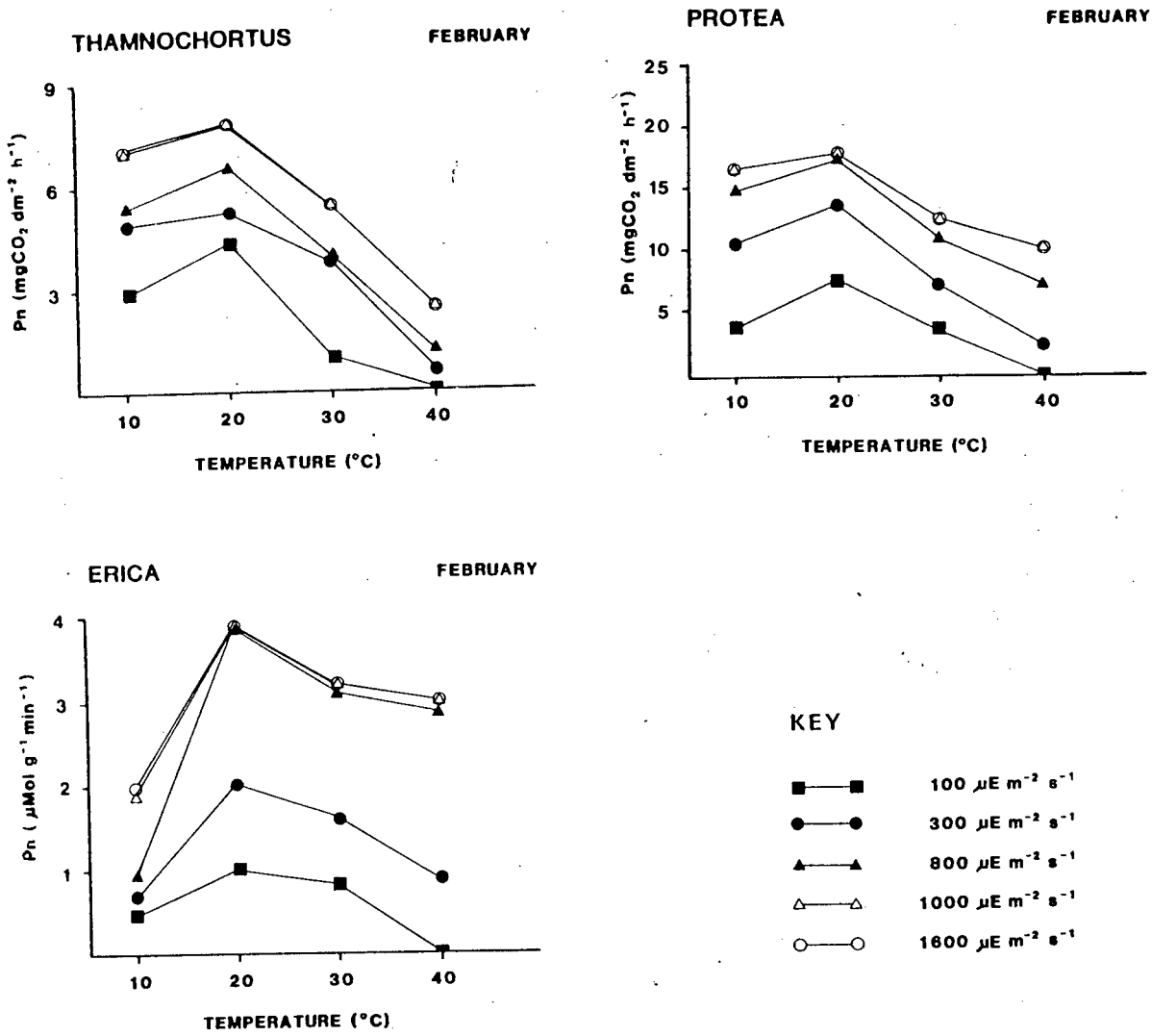


Fig.4.34: Temperature dependence of net photosynthesis of Thamnochortus lucens, Protea laurifolia and Erica plukenetii at five light intensities during February.

rates of Erica, however, were already saturated at 800 $\mu E\ m^{-2}\ s^{-1}$ (fig.4.42). At the higher temperatures (30 - 40°C), rates recorded for Erica were much lower at the low light intensities than at the saturating light intensities. Thamnochortus and Protea also exhibited depressed rates at the higher temperatures during February. The average photosynthetic rate at 10°C was circa 80% of the maximum rate recorded for each light intensity while rates at 40°C represented only circa 40% of the maximum.

Results obtained during November

All species studied during November (fig.4.41) showed photosynthetic light responses characteristic of C_3-species i.e. at all temperatures, photosynthesis was light saturated well below full sunlight. The photosynthetic temperature dependence of Erica and Protea was over a relatively narrow range with maximum activity reached near 20°C. In addition, rates recorded at the higher temperatures (30 - 40°C) were appreciably less than rates recorded at 10°C. This pattern was more marked for Erica. The photosynthetic temperature optimum for Thamnochortus during November (Fig.Y.a) was circa 30°C. Photosynthetic rates recorded at this temperature remained considerably higher at most light intensities. At 100 $\mu E\ m^{-2}\ s^{-1}$, however, the measured rates at 30°C were comparable to those recorded at the lower temperature regimes.

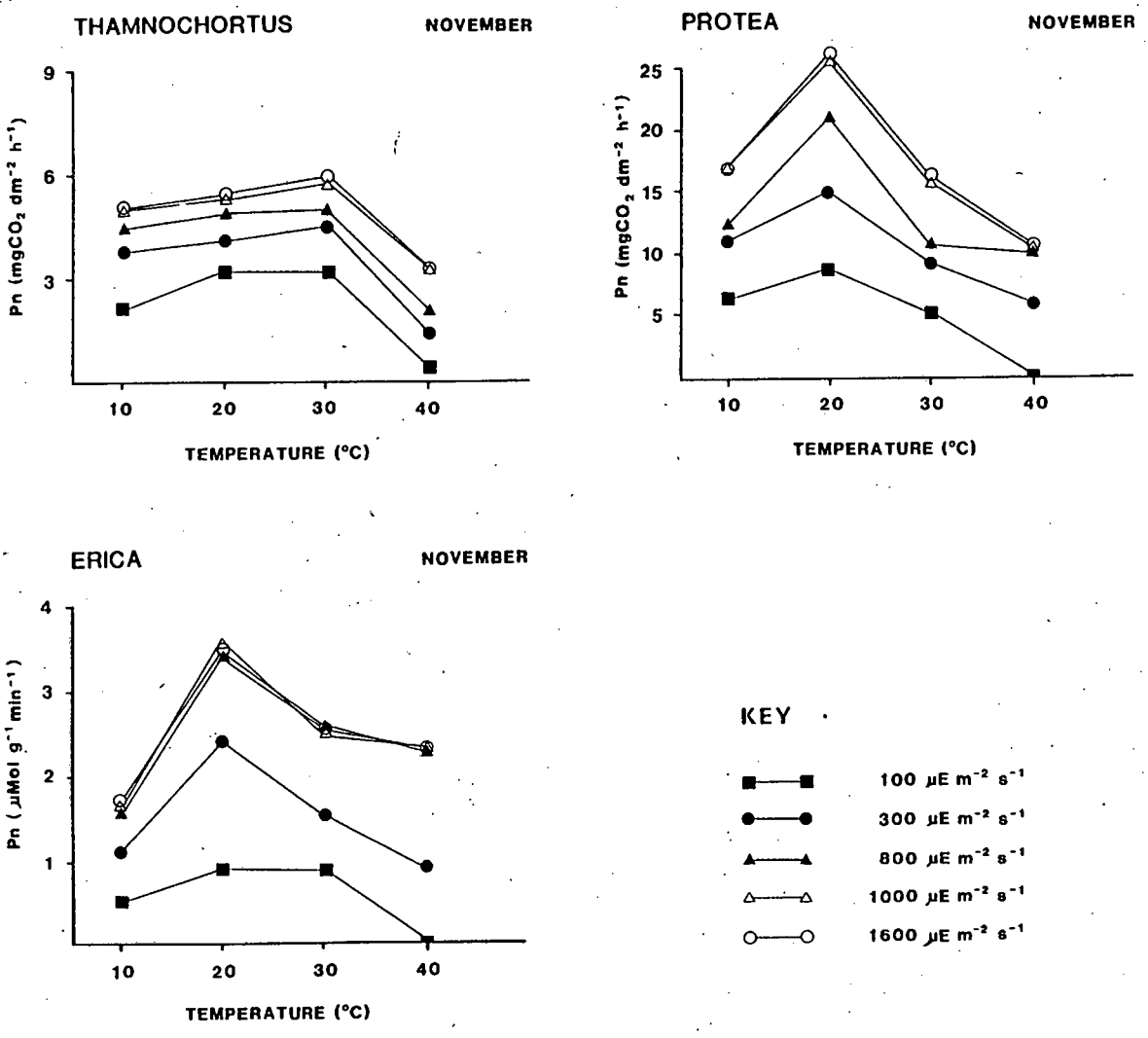


Fig.4.35: Temperature dependence of net photosynthesis of Thamnochortus lucens, Protea laurifolia and Erica plukenetii at five light intensities during November.

The relationship between temperature, irradiance and photosynthesis obtained for the species studied appear to be typical of the responses reported by Oechel et al.(1981a) for a number of mediterranean-climate sclerophyllous species i.e. light saturation occurred well below full sunlight and high photosynthetic rates were maintained over a relatively broad range of temperatures. The photosynthetic response to different irradiance levels were similar to those found by Mooney et al.(1983) for members of the South African Proteaceae.

The temperature response patterns of the fynbos species indicate that they are well adapted to temperature ranges experienced in their natural surroundings. Their low light requirement could be related to their intrinsic low photosynthetic capacities. Light saturation of Erica plukenetii was recorded at somewhat lower intensities than the other species. The unique ericoid leaf structure with its different light reflectance and absorbance characteristics may explain the slightly different responses of Erica to irradiance.

The photosynthetic temperature optimum obtained for Thamnochortus was approximately 10°C higher in November than during February. This phenomenon was surprising in that it was not found in the other species studied. The shift in

photosynthetic temperature response, however, is not unusual since it is generally known that plants can adapt photosynthetically to changing environmental conditions. Temperature in particular is known to have a remarkable conditioning effect (Bjorkman et al., 1980). Such temperature acclimations can occur after long periods of time, like seasons, or after shorter periods of exposure (eg.24hours) to a new temperature regime (Lange et al., 1974). The literature provides evidence for the natural occurrence of such adaptations in response to seasonal changes in thermal regime (Lange et al.,1974). Physiological reasons have been proposed to explain this seasonal shift. For example, it has been suggested that the response of stomatal activity to various temperatures may change with different seasons (Drake & Salisbury, 1972). Photosynthetic acclimation to temperature has also been related to seasonal changes in respiratory rates (Chatterton et al.,1970). Others have showed a relation between carbonic anhydrase activity and a shift in photosynthetic response related to temperature (Downton & Slayter, 1972).

There could be numerous reasons to explain the occurrence of the shift in photosynthetic temperature response in Thamnochortus. Only speculative reasons for such changes are possible at this stage due to lack of experimental evidence. One such speculative possibility is based on decreases in ratios of physiological activities with age. A decrease in the ratio of photosynthetic CO_2 assimilation to respiratory CO_2 release

was demonstrated by Bazzaz (1974). The photosynthetic culms of Thamnochortus were relatively young (3 months) when measurements were performed in November. Plant meterial could then have experienced a higher photosynthesis to respiration ratio than when measurements were performed 3 months later. In February, when plant material was 3 months older, the possibly greater positive relation between temperature and respiration could have resulted in greater depressions of net photosynthetic rate, compared to younger tissue, with similar increases in temperature. The reduced photosynthesis in relation to temperature, because of age induced higher respiratory rates, could then have caused photosynthetic saturation at lower temperatures resulting in a decreased temperature optimum for photosynthesis.

The exclusivity of the seasonal shift in photosynthetic temperature optimum to Thamnochortus could also be attributed to leaf temperatures. Unlike Erica and Protea species, the restiods do not have the structural or physiological means to maintain leaf temperatures close to ambient. Erica minimizes leaf temperature by virtue of leaf size and shape. Protea, on the other hand, keeps leaf temperatures to a minimum by transpirative cooling which is realized by its ability to tap water sources unavailable to most species. Thamnochortus, however, experienced a greater range of temperatures because of inefficient or no means to regulate leaf temperatures and

consequently needs to have photosynthetic machinery which can acclimatize more easily to temperature.

4.5 PHOTOSYNTHETIC RESPONSE TO IRRIGATION

The methodology used to determine the photosynthetic response to irrigation is described in section 3.5. From 21 to 26 February 1987, 15 individuals of each species were irrigated with tap water. Gas exchange measurements were performed on 5 individuals of both irrigated and unirrigated (control) treatments of each species. Measurements were performed on a cloudless day at five to six intervals during the day. Each value in the figure series 4.36 to 4.39 is the mean of 5 replicate measurements and the corresponding vertical bar represents the standard error of the mean (SEM). The absence of a vertical bar signifies that the SEM is too small to show on the scale of the graph.

Photosynthetic Rate

All results are expressed as averages of 5 measurements. Photosynthesis in both Erica and Protea (fig.4.36) was unaffected by additions of water, whereas Thamnochortus (fig.4.36) experienced a 20 - 40% increase in photosynthetic rate when supplied with water. A midday depression in photosynthetic rate (Pn) was observed for the irrigated and control treatments of Erica and Thamnochortus. Photosynthetic rate of Protea remained constant for both treatments throughout the day.

Transpiration Rate

There was a general tendency in all treatments for a gradual

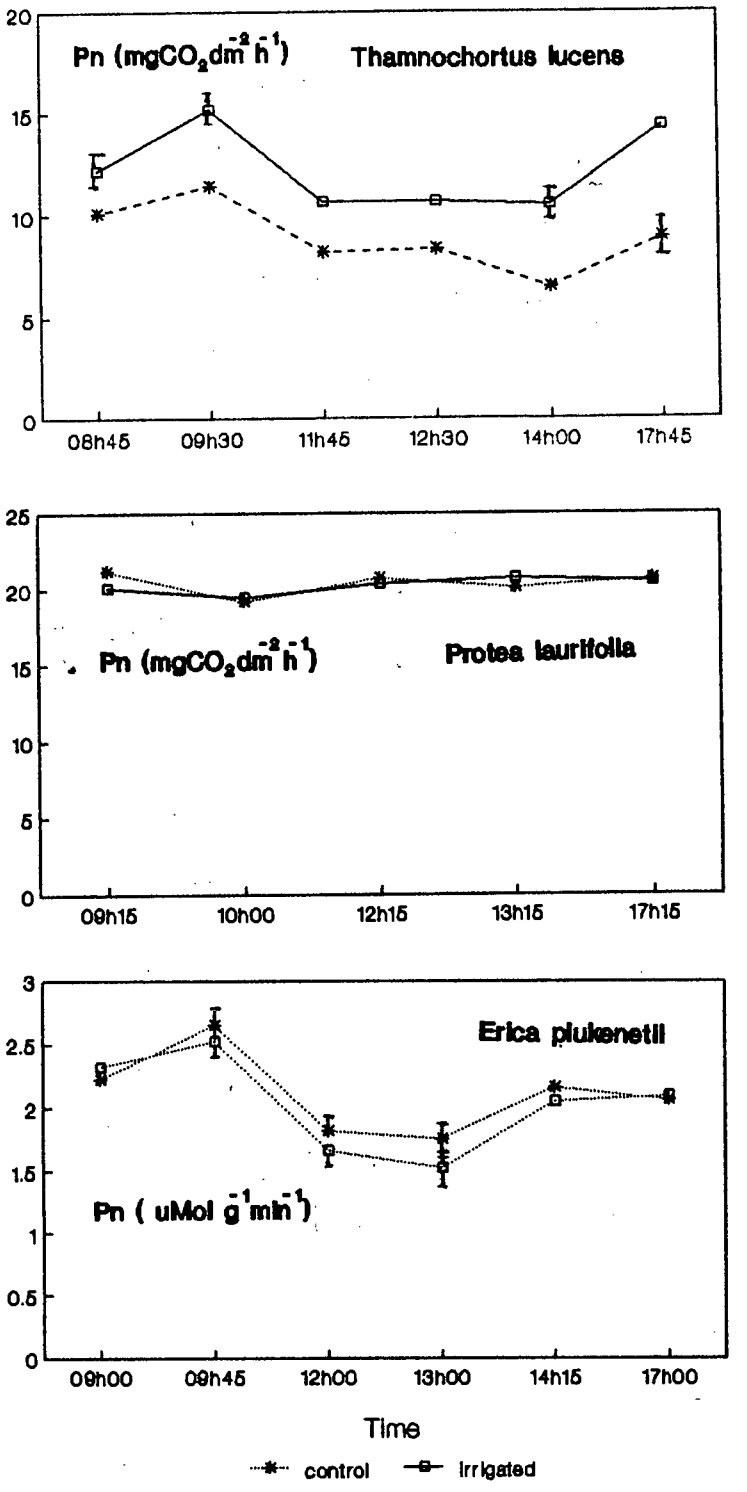


Fig.4.36: Diurnal variation in net photosynthetic rate of irrigated and unirrigated (control) individuals of Thamnochortus lucens, Protea laurifolia (juvenile) and Erica plukenetii during February 1987.

increase in transpiration rate (Tr) over the course of the day. This increase was less pronounced in both treatments (control and irrigated) of Erica (fig.4.37). Similar to the response of net photosynthesis, irrigation did not affect the Tr of Erica and Protea (fig.4.37). The rates recorded for Thamnochortus (fig.4.37), however, were approximately 25% higher for the irrigated individuals.

Stomatal Conductance

No differences were found in stomatal conductances (Gs) of the irrigated and the control treatments of Protea (fig.4.38). A 20% decrease in Gs was recorded at midday for both treatments of Protea . The stomatal conductances determined for Thamnochortus (fig.4.38) were always higher in the irrigated treatment. The irrigated treatment of Erica (fig.4.38), however, showed higher stomatal conductances than the control plants only during the morning.

Transpiration Ratio

The transpiration ratio ($mgH_2O/mgCO_2$) was also calculated for all treatments as the amount of water lost through transpiration per unit of photosynthetically fixed CO_2. Transpiration ratios (TR) of Erica (fig.4.39) and Protea (fig.4.39) were not changed by additions of water whereas the TR of Thamnochortus (fig.4.39) was higher in the control treatment than in the irrigated treatment. The difference in TR between the two treatments of Thamnochortus was more pronounced towards the end of the day.

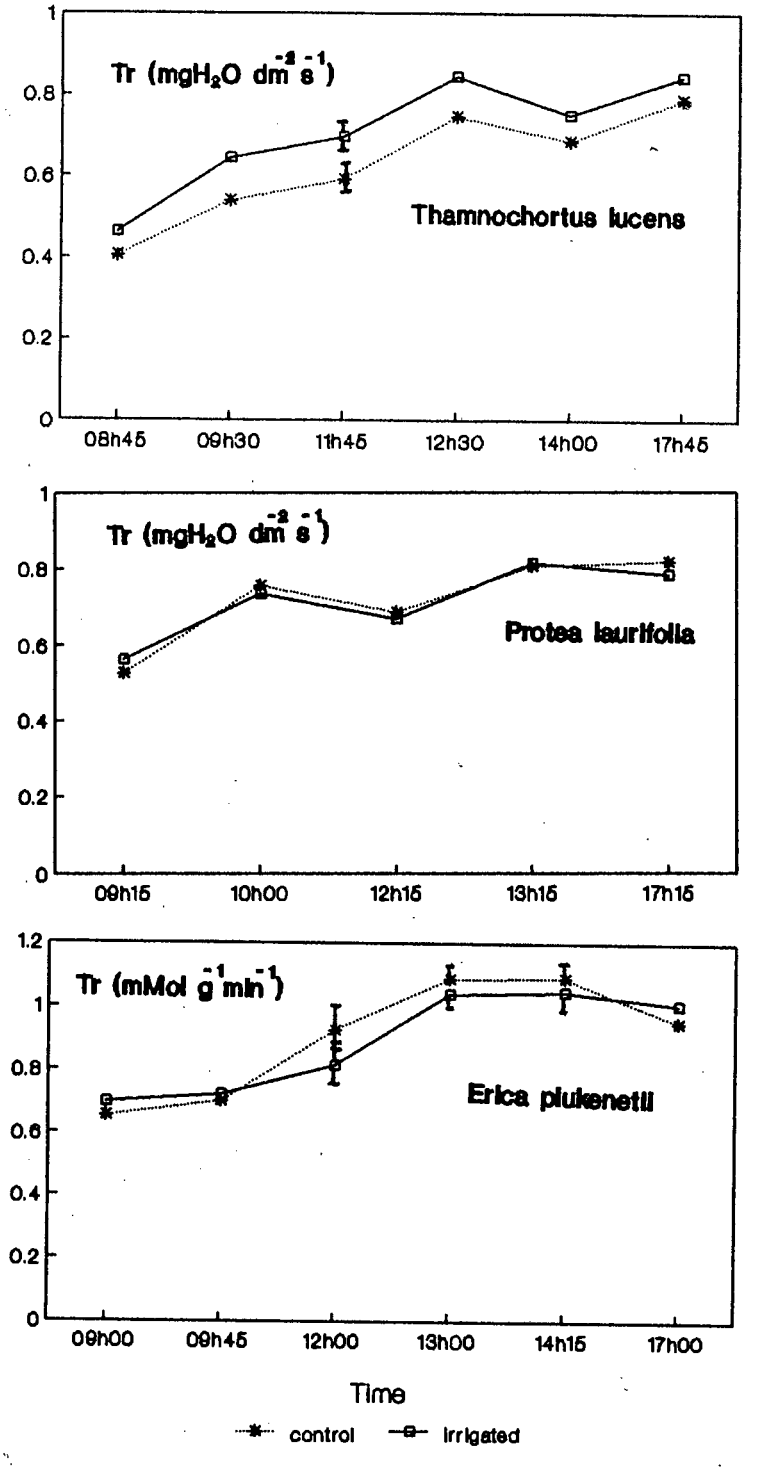


Fig.4.37: Diurnal variation in transpiration rate of irrigated and unirrigated (control) individuals of Thamnochortus lucens, Protea laurifolia (juvenile) and Erica plukenetii during February 1987.

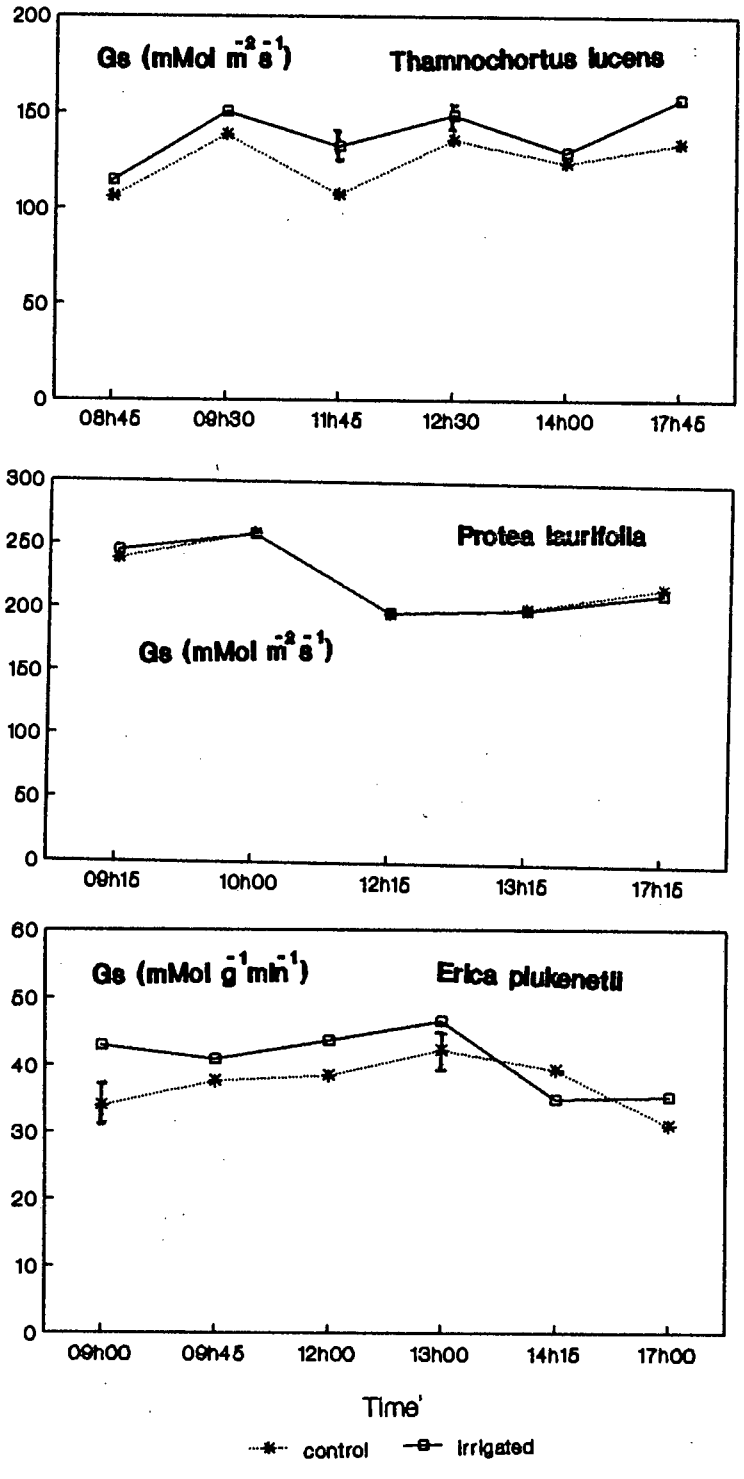


Fig.4.38: Diurnal variation in stomatal conductance of irrigated and unirrigated (control) individuals of Thamnochortus lucens, Protea laurifolia (juvenile) and Erica plukenetii during February 1987.

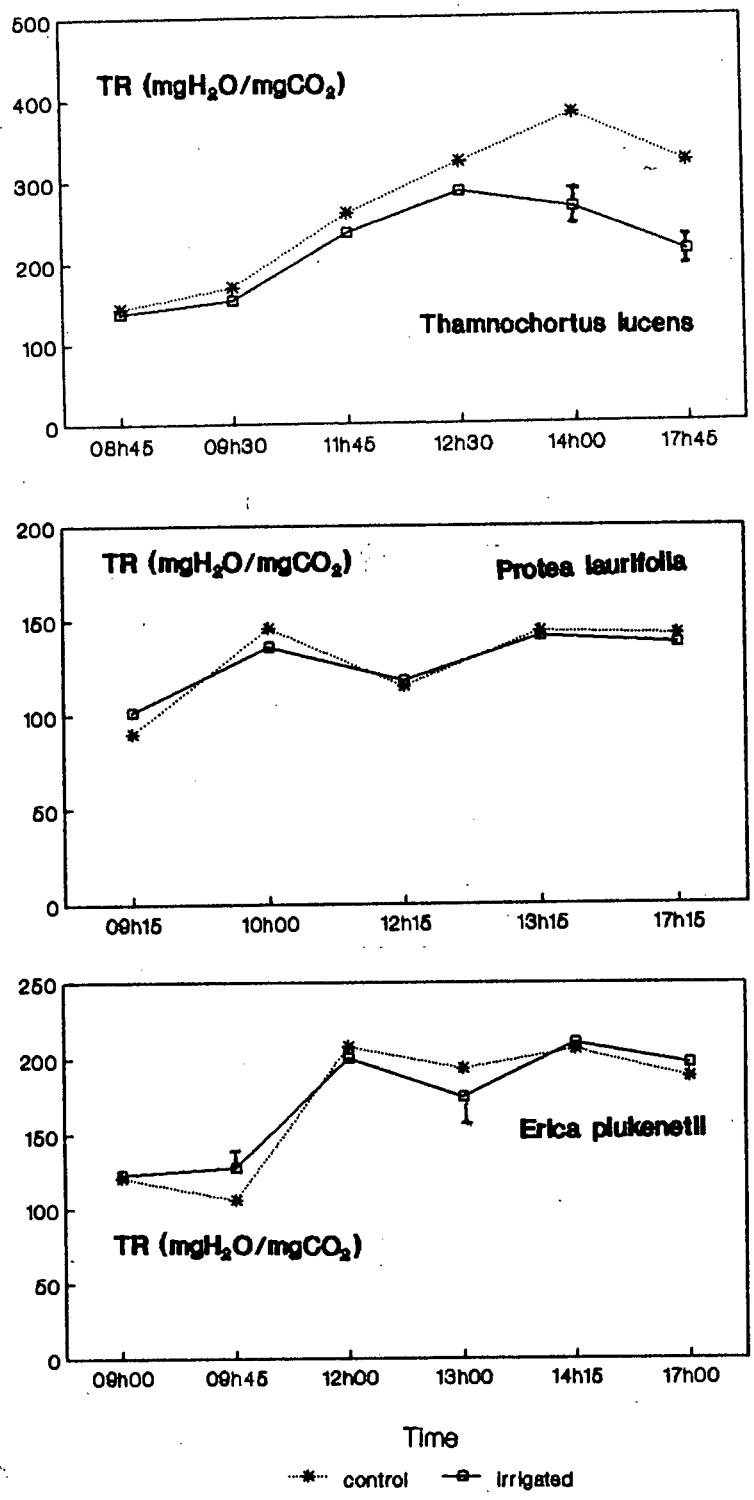


Fig.4.39: Diurnal variation in transpiration ratio (TR) of irrigated and unirrigated (control) individuals of Thamnochortus lucens, Protea laurifolia (juvenile) and Erica plukenetii during February 1987.

The effect of irrigation on rates of photosynthetic gas exchange has been studied for a few mediterranean-climate sclerophyllous species in California. Gigon (1979) found that drought-deciduous mesomorphic species were photosynthetically more responsive to irrigation than the evergreen scleromorphic shrubs. The present study of the response of fynbos growth forms, however, was of a less extensive nature. Water was applied only a few days before the responses were investigated. Nevertheless, the results provide some insight into aptive strategies of fynbos growth forms.

During February, at the time when measurements were made, all control plants experienced high photosynthetic rates which were comparable to maximum rates obtained in a study of the seasonal patterns of photosynthetic gas exchange (section 4.2).

Thamnochortus lucens

Photosynthetically, Thamnochortus was the most responsive to different levels of soil water. Irrigation resulted in substantial elevations of photosynthetic rate, transpiration rate and stomatal conductance. This behaviour was in contrast to the responses of Erica and Protea which were mostly unaffected by water additions. There could be several reasons to explain this phenomenon. Firstly, this species has a shallow

rooting system. At the time of irrigation, the water content of the upper soil layers, in which Thamnochortus roots are found, was probably below that required for maximum photosynthesis. Consequently, this species experienced some degree of soil water shortage. Irrigation resulted in hydroactive increase in stomatal conductance which led to elevated rates of C-fixation and transpirational water loss.

Protea laurifolia

Practically no differences were observed between the photosynthetic rates of the control and the irrigated treatments. The rates of transpiration, stomatal conductances and the calculated values of TR were also unaffected by additions of water. One of the adaptations responsible for the absence of these responses could be the deep and extensive rooting systems enabling water uptake from deeper soil horizons. Although Pn of both treatments remained constant throughout the day (fig.4.44), the transpiration rates (fig.4.47) and particularly the stomatal conductances (fig.4.50) exhibited depressions at midday. This suggests that diurnal patterns of gas exchange of this deep-rooted species were influenced by factors other than water availability (eg. temperature and humidity factors).

Erica plukenetii

Erica did not show any photosynthetic response to water additions at the time when readings were taken. Photosynthetic

and transpiration rates of the irrigation treatment and of the control were comparable in diurnal pattern and in the values obtained at each time during the day (figs. 4.36 & 4.37). During the morning, the stomatal conductances, however, were found to be appreciably higher for the irrigated treatment than for the control plants. The elevated stomatal conductances of the irrigated plants did not result in concomitant increases in Pn. This suggests that internal factors like mesophyll resistances were of more importance than stomatal conductance in determining rates of C-fixation at the time of measurement.

Initial investigations revealed that Erica roots at the 3 to 4 year old plant age were comparable to Thamnochortus rooting systems in the soil depth reached by each rooting system. Both species can therefore be considered as shallow-rooted. Erica , however, did not respond to water additions in a similar way to Thamnochortus because the former apparently has morphological adaptations to limit water loss. Morphological characteristics like leaf shape and leaf size as well as limited stomatal distribution could be considered as adaptations which prohibit excessive water loss.

4.5 SEASONAL VEGETATIVE GROWTH STUDIES

One of the objectives of the present study was to relate seasonal variations in carbon assimilation to periodicity of plant vegetative growth. Although it has been shown in previous studies that root growth represents an appreciable drain on carbon reserves, for practical reasons only above-ground plant growth was considered. Oechel & Lawrence (1981), for example, have shown that 65% of the carbon fixed during photosynthesis is utilized by stems and leaves of the chaparral shrub, Arctostaphylos glauca. The roots of this species sequestered about 34% of the annual carbon uptake. The approach adopted in this study of relating carbon fixation to seasonal growth may be critisized as being superficial since it is known that carbon allocation patterns present a more accurate interpretation of seasonal phenological phenomena (Oechel & Lawrence, 1981). It should, however, provide some understanding of plant behaviour in the fynbos in response to seasonal variations in photosynthetic capacity.

The methods which were employed are dicussed in section 3.7. The results are shown in figures 4.40 to 4.47. Each value in the figure series is the mean of 10 to 15 measurements and the corresponding vertical bar represents the standard error of the mean.

Intra-specific variations were large. It was nevertheless still possible to identify definite periods of growth. High variation in values obtained when measuring monthly shoot increments is one of the problems common to most phenological studies (Pierce, 1984).

Ericoid species

At the time of shoot labelling at the beginning of the study period (October 1985) both Erica plukenetii (fig.4.40) and Erica hispidula (fig.4.41) experienced shoot elongation. E.hispidula ceased growth in December 1985. E.plukenetii, however, exhibited shoot elongations up to January 1986. The mean shoot elongation for E.plukenetii during January was 4mm with some individuals not showing any increases in length. No growth occurred for both species from February to June. Shoot elongation commenced again during July for E.hispidula with a maximum monthly increase recorded during the September-November interval. E.plukenetii experienced another growth phase from September to the end of the sampling period during December 1986. E.plukenetii also experienced a maximum monthly increase during the September - November period. The relative extent of the rooting systems of E.plukenetii and E.hispidula is unknown which renders it difficult to interpret the differences in seasonal growth patterns.

Restioid species

Culm development and growth were similar in both sexes of

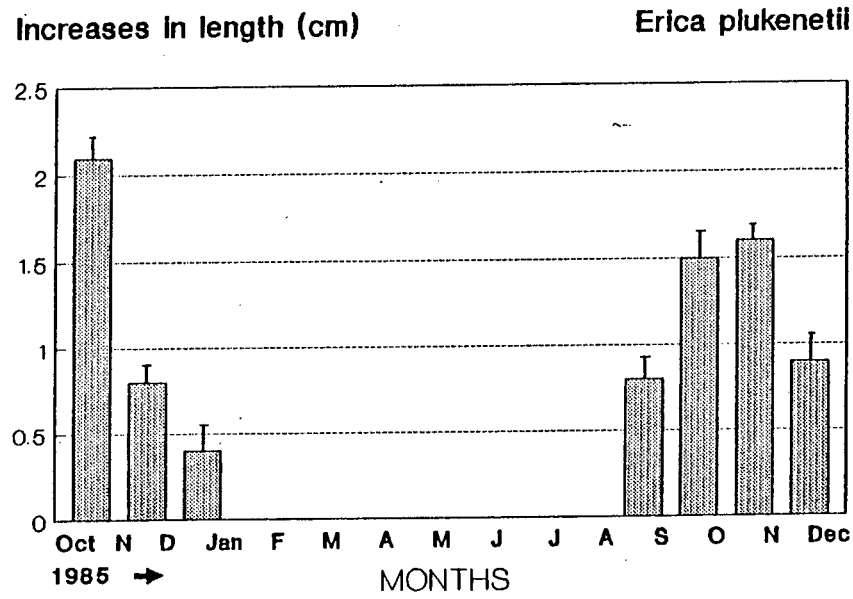


Fig.4.40: Monthly increases in shoot length of Erica plukenetii from October 1985 to December 1986. The vertical bars represent the standard errors of the mean.

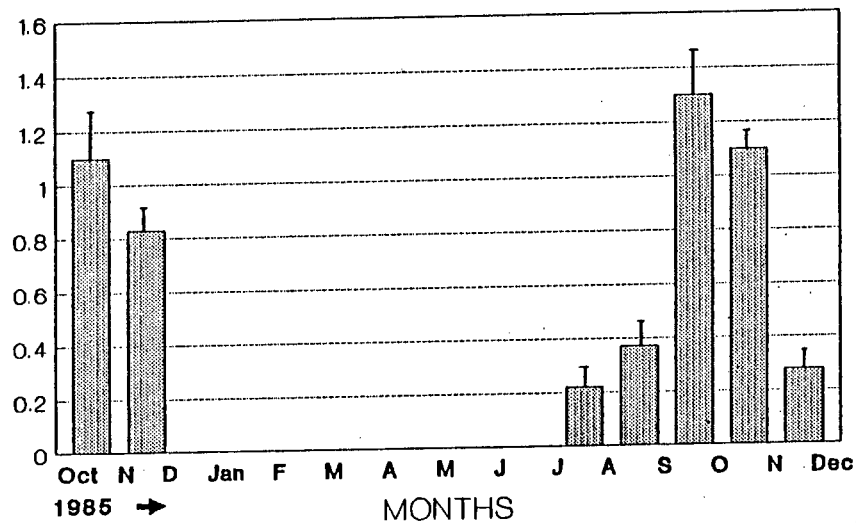


Fig.4.41: Monthly increases in shoot length of Erica hispidula from October 1985 to December 1986. The vertical bars represent the standard errors of the mean.

Thamnochortus lucens (fig.4.42) and Askidiosperma paniculatum (fig.4.43). Although A.paniculatum experienced greater increases in growth during a particular month, there were no significant differences in the seasonality of culm elongation between the two species. Tagged culms of both species showed decreases in rates of monthly shoot elongations from October 1985 (start of study period) to December-January when growth stopped. During this period inflorescences were produced which developed to maturity only after monthly elongation ceased to occur. New culms emerged during the May-June interval for T.lucens and A.paniculatum. New labels were applied during June 1986 and monthly shoot elongations were again measured from July onwards. Shoot elongations continued in both species until the end of the study period in December. A maximum in monthly increments was reached from August to September for T.lucens. During this period a mean value of 13cm was recorded. For A.paniculatum, a maximum monthly increase in shoot length of 21cm was measured from October to November.

For both species culm development occurred exclusively from May to January with maximum elongation taking place during spring. The results for these species are consistent with observations by Sommerville (1983) who recorded a similar spring-summer growth for the restioid species Thamnochortus punctatus and Restio monanthus.

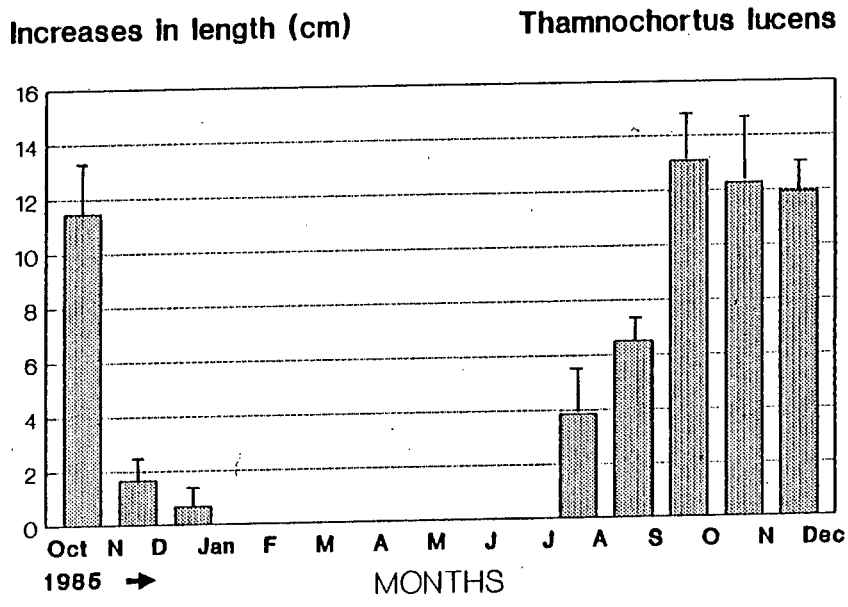


Fig.4.42: Monthly increases in culm length of T.lucens from October 1985 to December 1986. The vertical bars represent the standard errors of the mean.

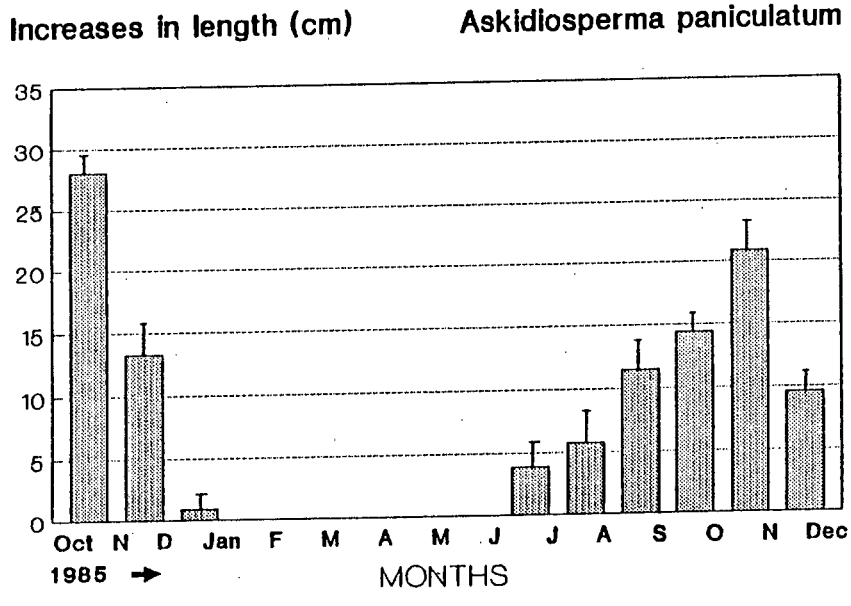


Fig.4.43: Monthly increases in culm length of A.paniculatum from October 1985 to December 1986. The vertical bars represent the standard errors of the mean.

Broad-leaf species

The mature and juvenile individuals of Protea laurifolia (figs.4.44 & 4.45) exhibited significant seasonal differences in shoot elongation during 1985 and 1986. During 1985, shoot growth of the juvenile individuals terminated in December while during 1986 growth only occurred until November. The mature plants experienced growth from August to November during 1986, while shoot elongation was recorded up to January during the previous growing season. Differences between the juvenile and mature individuals of P.laurifolia with regards to the magnitude of shoot elongation, the timing of growth and the month of maximum growth suggest that plant age affects growth patterns. The shifts in the growing season between 1985 and 1986 could be attributed to differences in the rainfall patterns during these years.

Shoot elongation of Metrosideros angustifolia (fig.4.47) occurred from June to January with maximum increases in shoot length recorded from October to December. Leucadendron salignum (fig.4.46) experienced shoot growth from November to March. Shoot elongation was most rapid from December to February.

Comparisons between species

All species which were investigated grew to some extent during spring although spring did not necessarily represent the period of maximum growth. Only M.angustifolia and L.salignum experienced their highest growth rates during the summer

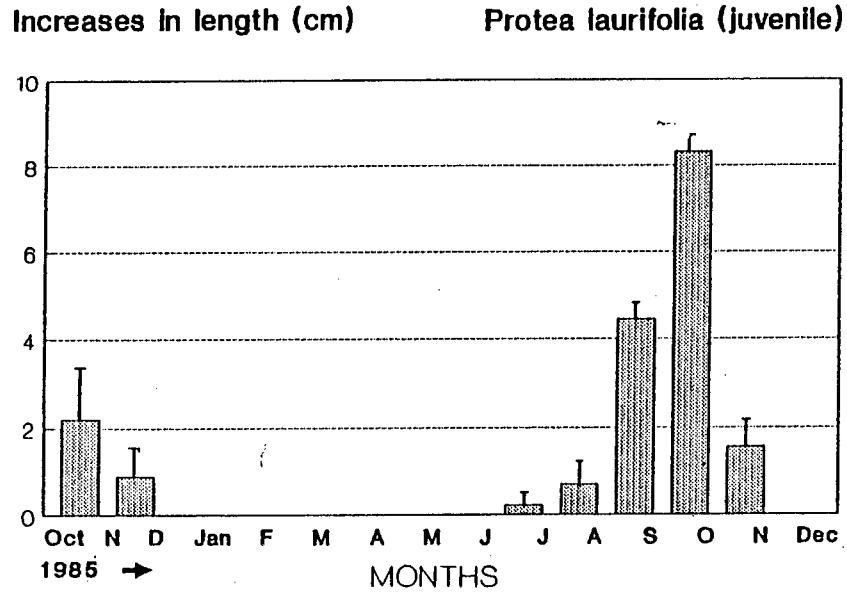


Fig.4.44: Monthly increases in shoot length of P.laurifolia (juvenile) from October 1985 to December 1986. The vertical bars represent the standard errors.

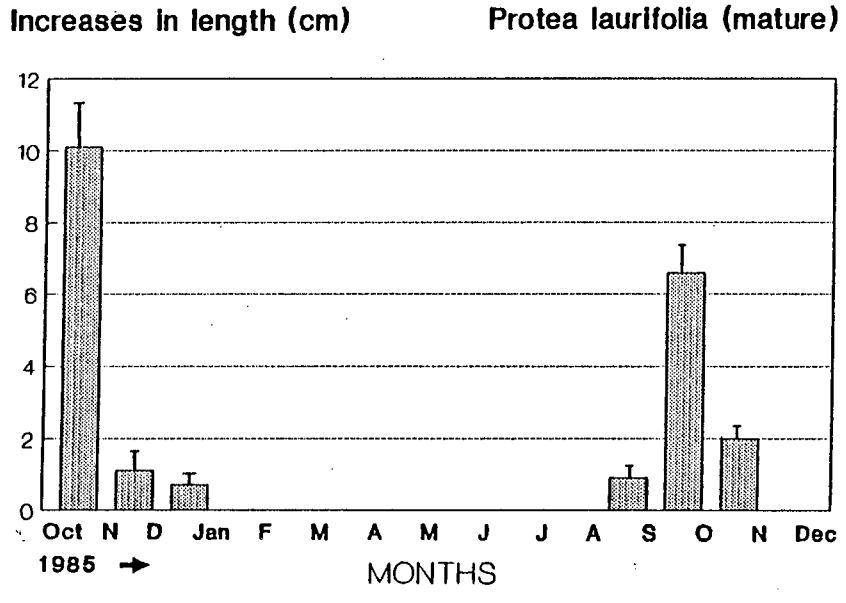


Fig.4.45: Monthly increases in shoot length of P.laurifolia (mature) from October 1985 to December 1986. The vertical bars represent the standard errors.

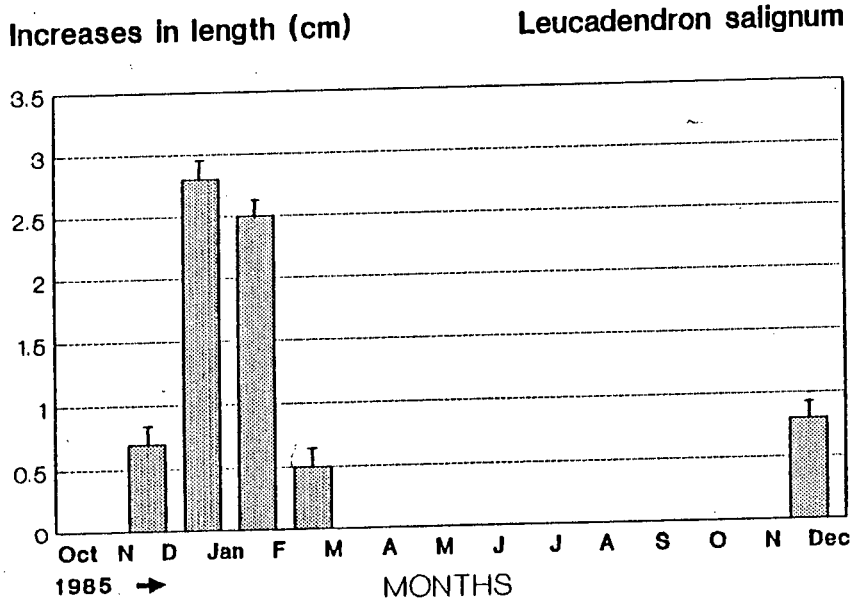


Fig.4.46: Monthly increases in shoot length of L.salignum from October 1985 to December 1986. The vertical bars represent the standard errors of the means..

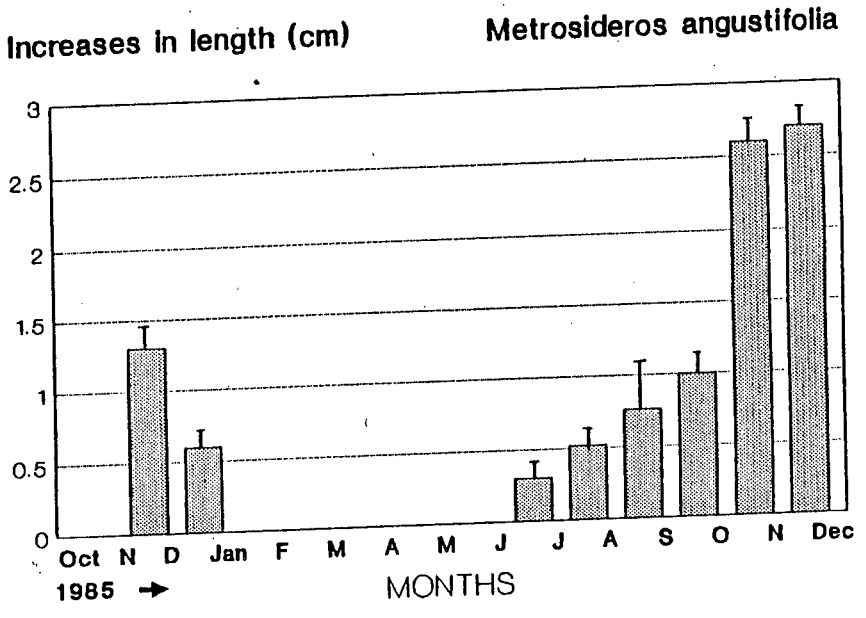


Fig.4.47: Monthly increases in shoot length of M.angustifolia from October 1985 to December 1986. The vertical bars represent the standard errors.

months. Furthermore, L.salignum was the only species which exhibited growth during early autumn (February - March). These species have the advantage of having soil water available during periods when other deep-rooted species are possibly subjected to periods of water shortage. L.salignum, being a resprouter after fire, has an extensive tap root system. In contrast to re-seeders like P.laurifolia, it probably has a much higher root to shoot ratio and consequently has more soil water available in relation to potential transpirational surfaces. The advantage of having a more extensive rooting system was probably more pronounced at the 3-4 year plant age (after fire) at which the measurements were taken. M.angustifolia possibly has more soil water available during the summer months because it grows exclusively along stream banks. Other researchers in this field have also recognized the possible relation between rooting habit and seasonal growth rythms (Mooney & Dunne, 1970; Sommerville, 1983).

E.plukenetii and E.hispidula grew for the most part during spring and to some extent during early-summer. In contrast to the values recorded for the restioid species, monthly increases in shoot length were very low. The difference in magnitude of monthly increments of new tissue between the two growth forms is possibly related to their respective adaptive strategies. The restioid species could be considered as being pseudo-deciduous species since all culms during their second year became senescent. Unlike the ericoid species the restioids apparently

do not invest in photosynthetic organs with long life-spans. The restioids need to produce new photosynthetically active material every year. In contrast, the true evergreen ericoids possibly allocate much more carbon and energy to the structure and maintenance of their photosynthetic organs and less to the production of new tissue. The ericoid species therefore experience shoot elongations of much lower dimensions. Despite the differences in rates of growth, there is a striking correlation between these two growth forms in terms of their rooting habits and season of shoot or culm growth. All the species are considered as being shallow-rooted and growth occurred principally during spring. Spring growth was presumably in respone to higher temperatures and to adequate soil water before the onset of the summer period of assumed water stress.

4.8: SEASONAL CARBON GAIN

The photosynthetic capacities of the fynbos species investigated generally reached maximum values from winter to spring (section 4.2). However, preliminary studies (section 3.7) have shown that low irradiance levels, caused by heavy cloud cover, strongly reduced photosynthetic capacity, sometimes resulting in zero Pn. This would considerably limit carbon gain during months which experience high incidences of cloudy days. Consequently, the months in which the highest photosynthetic capacities were recorded do not necessarily represent the most productive periods of the year. The average monthly carbon gain (AMCG) was therefore estimated for some of the species to determine which months of the year could be considered as the most productive for the various growth forms. AMCG was calculated using the following data: number of cloudless days per month, length of daylight and average monthly photosynthetic capacity.

Cloud cover data collected at Hawequas weather station ($33^{o}\ 44^{1}$ S : $10^{0}\ 4^{1}$ E) from April 1983 to April 1986

were used to estimate the number of cloudless days per month (K) (Appendix Table 2). It was assumed that the species studied did not photosynthesize under conditions of heavy cloud cover (refer to section 3.7).

Daylight (D) was determined using standard metereological tables (Appendix Table 3) (List, 1984). The author defined daylight as "the interval between sunrise and sunset. The latter are considered to occur when the upper edge of the disk of the sun appears to be exactly on the horizon with an unobtrused horizon and normal atmospheric refraction."

The average Pn measured at the three times of the day (refer to section 4.2) was used as an index of the monthly photosynthetic capacity (PC). Average monthly carbon gain (AMCG) was then calculated as follows:

K (no. of cloudless days) x D (length of daylight) x PC

= AMCG (units : $mgCO_2\ dm^{-2}\ month^{-1}$ or $\mu Mol\ g^{-1}\ month^{-1}$)

On the basis of their calculated AMCG's, the species studied can be grouped into two principal categories. The shallow-rooted T.lucens and E.plukenetii (fig.4.48) experienced their lowest AMCG during the summer months and

their highest AMCG during spring. In contrast, the deep-rooted P.laurifolia, L.salignum and M.angustifolia would appear to fix most of their carbon during summer (fig 4.49). Some environmental factor encountered during summer limited photosynthetic carbon gain of the shallow-rooted species to much greater extents than that of the deep-rooted species. It was established previously (section 4.2) that water shortage during summer could not have been the only and most important factor causing the summer decline in Pn of the shallow-rooted species.

The monthly variation in carbon gain and the observed vegetative growth rythms (section 4.7) provide correlations in some instances. E.plukenetii, for example, would appear to assimilate most of its carbon from September to November (fig.4.48), at a time when maximum aboveground growth rates were recorded (fig.4.40). Similarly, L.salignum experienced maximum AMCG (fig.4.49) as well as maximum stem elongation (fig 4.46) from December to February. From these findings it appears that these two species invested a major portion of their photosynthates produced during the most productive part of the year to growth and development.

The occurrence of maximum vegetative growth and maximum AMCG

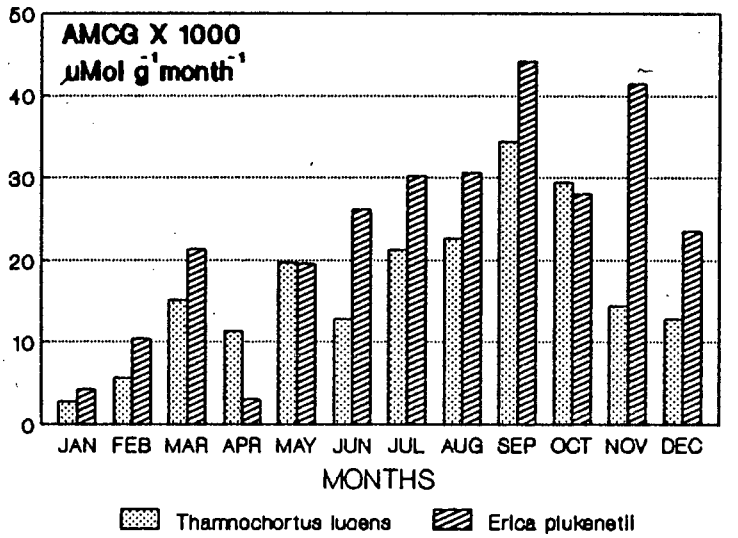


Fig.4.48: The seasonal variation in average monthly carbon gain (AMCG) of. Thamnochortus lucens and Erica plukenetii.

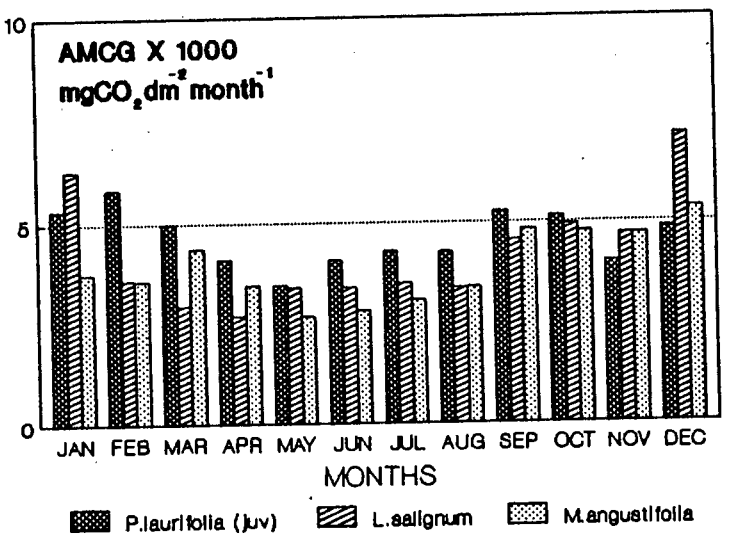


Fig.4.49: The seasonal variation in average monthly carbon gain (AMCG) of Protea laurifolia, Leucadendron salignum and Metrosideros angustifolia.

was not as well synchronized for T.lucens as it was for E.plukenetii and L.salignum. Whereas maximum culm elongation of T.lucens occurred from September to December (fig.4.42), AMCG reached its highest values from August to October (fig.4.48). Aboveground growth therefore did not occur at the expense of currently produced photosynthates. It is likely that stored photosynthates were important in providing building materials during periods of culm development.

It is tempting to suggest that the summer growth observed for many fynbos species (Pierce, 1984; Sommerville, 1983) can be attributed to maximum carbon gain occurring during summer. Unfortunately, no data are available on the utilization of photosynthates produced during various months of the year.

CHAPTER 5: GENERAL DISCUSSION AND CONCLUSIONS

One of the principal aims of this investigation was to determine the photosynthetic capacities of mountain fynbos plant growth forms. On the basis of the field observations two distinct groups can be distinguished i.e. the ericoid and the restioid species which exhibited relatively low photosynthetic rates and the proteoid species and Metrosideros angustifolia on the other hand, which experienced comparatively high photosynthetic rates throughout the year. The magnitude of the differences in Pn capacities of the two groups becomes apparent if the rates of three representative species are expressed on a dry weight basis (Appendix Figure 1): the rates of photosynthetic C-fixation of Protea laurifolia (juvenile) were always more than double the rates recorded for the three year old individuals of Thamnochortus lucens and Erica plukenetii.

Another objective was to establish the seasonal patterns of photosynthetic C-fixation. Most species experienced declines in Pn during summer. Maximum photosynthetic rates were recorded during spring and winter. The only exception in this regard was

L.salignum which experienced maximum photosynthetic rates during summer. The degree of decline in photosynthetic rates during summer was much more pronounced for the ericoid and restioid species than for M.angustifolia and P.laurifolia (juvenile and mature).

The species studied can similarly be separated on the basis of rooting depth. The roots of the ericoid and restioid species were restricted to the upper soil horizons while the roots of the proteoids and M.angustifolia were found in much deeper soil layers. It was possibly no coincidence that the shallow-rooted species maintained the lowest photosynthetic capacities and that they experienced the greatest decline in Pn during summer. In contrast, the deep-rooted species maintained the highest photosynthetic capacities and they experienced little or no summer depressions in Pn. It is of special interest that A.paniculatum, a restioid species with a more extensive rooting system than T.lucens, exhibited a seasonal Pn pattern which did not coincide with the observed patterns of the shallow-rooted species.

Since the shallow-rooted species experienced the greater decline in xylem pressure potential (more negative values) during summer it appears reasonable to assume that their lower photosynthetic capacities and their greater summer decline in Pn can be

explained in terms of water stress. Harrison et al.(1971) have also found a relationship between rooting depth and photosynthetic carbon assimilation of mediterranean-climate plant communities of California. The authors have reasoned that a deep and extensive rooting system allows access to a larger store of soil water, thereby avoiding a large decline in Pn during summer drought. However, the results obtained for the fynbos species did not produce sufficient evidence to confirm that rooting depth and plant water status in the fynbos are related to photosynthetic capacities. The correlations between the measured xpp's and Pn's were not statistically significant for any of the species studied. However, the coefficients of correlation were greater for the shallow-rooted species than for the deep-rooted species (Appendix Table 1) which suggests that if plant water status had an effect on photosynthetic processes, it would be of greater importance in determining the Pn's of the shallow-rooted ericoids and T.lucens.

Because T.lucens exhibited the lowest photosynthetic rates of the species studied it was anticipated that this plant would respond immediately to short-term changes in the environmental factors. An experiment carried out to determine if mountain fynbos growth forms were limited photosynthetically by low soil water levels during summer has indeed shown that T.lucens

experienced increased stomatal conductances and elevated photosynthetic rates when irrigated. In contrast, E.plukenetii and P.laurifolia (juvenile) did not respond to irrigation during summer. T.lucens would therefore be expected to benefit from short irregular periods of rain.

Attempts to interpret the seasonal changes in net photosynthetic rate can be problematic if field observations of only Pn and one other variable (xpp in this case) are used. In addition to xpp, numerous environmental and plant internal physiological factors are also subject to seasonal changes and they have all been shown to have effects on photosynthetic capacity.

Investigations of the photosynthetic temperature response of T.lucens, E.plukenetii and P.laurifolia (section 4.5) have shown that during summer the net photosynthetic rate of these species were severely depressed at temperatures above 20°C. Since the air temperatures measured during the summer months were frequently more than 25°C (Appendix Table 4), the depressed Pn's observed during summer (section 4.2) could have been due to the effects of high temperature on net photosynthetic rates as is shown in section 4.5. It is likely that the higher temperatures could have been responsible for increases of photorespiratory rates (characteristic of C_3 species), thereby reducing net photosynthetic rate.

Statistical analyses have shown that the observed xpp's of the shallow-rooted species correlated significantly with their measured transpiration rates and stomatal conductances (sections 4.2 & 4.3). This indicates that stomatal conductance and rates of transpiration of these species were responsive to changes in plant water status. This was not the case for the deep-rooted species.

The diurnal patterns of photosynthetic C-fixation, transpiration and stomatal conductance showed a great variety of shapes. Generally during spring and winter, most plants exhibited what Hellmuth (1971) described as "one-peak" patterns. Maximum photosynthetic rates and transpiration rates were observed during midday (i.e. a single peak), possibly because of maximum stomatal aperture. During summer, a "two-peak" pattern (also described by Hellmuth, 1971) occurred for many species i.e. midday depressions in photosynthetic gas exchange with elevations during the morning and late-afternoon. The observed decrease in stomatal conductance during midday possibly caused the reduction in CO_2 diffusion and water loss, thus limiting photosynthetic C-fixation and transpiration rate. However, it is uncertain at this stage if midday stomatal closure was in response to the observed midday decreases in tissue water levels or in response to other stress factors such as high temperature.

One of the problems experienced in analyzing the diurnal patterns of photosynthetic gas exchange was the absence of detailed laboratory experimental data to explain the observed patterns measured in the field. Even more problematic were the numerous indications that the species studied responded differently to the diurnal changes in environmental factors. Moreover, there was always the possibility of interaction of various factors in eliciting a particular photosynthetic or stomatal response. More detailed experimentation is certainly required before it will be possible to uncouple the effects of various environmental and plant internal physiological factors on the sensitivity of photosynthetic gas exchange processes.

Analysis of the water use in relation to carbon fixation (transpiration ratio) provided a good insight into the mechanisms used by the various species in utilizing water as a resource. Essentially two principal mechanisms were identified. Firstly, those plants which lost minimum amounts of water in relation to carbon gain i.e. low transpiration ratios. These plants were possibly able to control excessive water loss (ericoids) or they maintained relatively high photosynthetic capacities throughout the year (proteoids). Another category, best represented by T.lucens, experienced very high transpiration ratios, particularly during summer. This species

can therefore be considered as being less attuned to conserving water.

The influence of different combinations of irradiance levels and temperature on net photosynthetic rate of representatives of the three major mountain fynbos growth forms was also determined. These experiments were carried out during summer and spring to investigate possible adaptations to naturally occurring seasonal changes in environmental conditions.

Light saturation of E.plukenetii was recorded at significantly lower photon irradiances than in P.laurifolia (juvenile) and T.lucens (section 4.5). The unique ericoid leaf structure with possibly different light absorbance and reflectance characteristics may explain the responses of E.plukenetii to irradiance. The temperature at which maximum photosynthesis was recorded (ca 20^{o}C), remained unchanged for P.laurifolia and E.plukenetii during both seasons. The photosynthetic temperature optimum obtained for T.lucens, however, was higher in November than during February. If the seasonal shift in temperature optimum for T.lucens is considered in the light of the natural changes in air temperature throughout the year then a possible adaptive advantage for such a temperature optimum controlling ability becomes apparent. The hottest periods of the year occur during summer and usually coincide with periods

of lowest precipitation. During this period, increases in stomatal conductance to assimilate more carbon would result in excessive water loss and ultimately dessication. During spring, when water is relatively non-limiting, T.lucens can afford to realize greater stomatal conductances at higher temperatures. The photsynthehtic capacity of the shallow-rooted T.lucens was shown to be intrinsically low and its annual carbon gain is further reduced by depressions in photosynthetic capacity during summer (section 4.2). The annual carbon gain of this species would therefore be aided by such a temperature conditioning effect.

AN ECOLOGICAL PERSPECTIVE:

It is commonly assumed that plant species with high C-fixation rates have the advantage of more available carbon which can be used in various ways (eg. reproductive and vegetative growth) to compete favourably during the successional stages after a disturbance (Solbrig & Orians, 1977; Mooney et al., 1975). In one of the first studies to investigate the relationship between plant success and photosynthetic capacity, Oechel and Mustapha (1979) provided support for the assumption that greater photosynthetic capacity is of an adaptive adavantage. These authors found a strong correlation between cover and

photosynthetic capacity across a geographical gradient of mediterranean scrub vegetation in southern California.

Testing of post-fire regeneration models on a range of fynbos communities (Moll & Hoffman, 1984) has shown that approximately 10 years after fire, the proportional representation of the ericoid and the restioid components declines, at which time the proteoid element is contributing an increasingly greater percentage to the total plant population. The photosynthetic data in this report uphold these findings. The greater carbon gain of the proteoid species and an ability to maintain high photosynthetic rates throughout the year could have some adaptive advantage in the later successional stages following a fire. Similarly, the low carbon gaining capacities of the restioid and ericoid species would put them at a disadavantage when plant density and consequently competition for resources increases. Because plants are spaced at distances further from one another during the early successional stages after fire, competion for resources, especially water, is minimal. This is possibly one of the factors which contributes to the dominance of the shallow-rooted species immediatly after a fire. The importance of factors related to phenological cycles and reproductive biology in the successional stages, however, cannot be overlooked and certainly are as much part of the processes which determine community structure in the successonal stages

after a disturbance such as fire.

Knowledge of plant photosynthetic response to environmental factors can be used to predict plant performance in a given habitat (Mooney, 1976).. For example, Mooney et al.(1975) were able to identify soil moisture as the environmental factor of overriding importance in limiting carbon gain of Heteromeles arbutifolia. Moreover, these authors also used their findings of carbon losses integrated with carbon gains in an attempt to understand the environmental factors which determine the population distribution of this species. Schulze et al.(1967) constructed annual carbon budgets to predict the distributional limits of Pinus aristata. The carbon balance approach of understanding plant success and distribution cannot be used for fynbos species since nothing is presently known of respiratory carbon losses. Furthermore, no data are presently available on the patterns of carbon utilization after it has been assimilated. Therefore, any discussion of the adaptive value of carbon gain can only be speculative.

In contrast to the responses of E.plukenetii and P.laurifolia, T.lucens exhibited elevations in rates of photosynthetic gas exchange when irrigated (section 4.6). The ericoid and proteoid species, however, did not show changes in photosynthetic activity upon irrigation. These findings suggest that during

periods when soil water levels are high, T.lucens experiences increased photosynthetic rates at the cost of rapid water loss. When water is not available, low plant water levels can apparently be tolerated without resulting in dessication. The relative inefficiency of the water loss controlling ability is possibly compensated for by dessication tolerance during periods of water shortage. These features of T.lucens appear to be excellent adaptations for survival and growth in sometimes very dry soils. An analysis of the distribution of vegetation structural characters in the mountains of the Cape (Campbell, 1985) showed that fynbos dominated by restioids is associated with very shallow and rocky soils. These soils are frequently subjected to low soil water levels. The unique characteristics of T.lucens identified above appear to be excellent adaptations for survival and growth in sometimes very dry soils and this would provide the physiological support for Campbell's findings.

Another unique feature observed for T.lucens is the ability to change its photosyntetic temperature optimum (section 4.5). P.laurifolia and E.plukenetii, however, maintained seemingly constant photosynthetic temperature optima during spring and summer. It was hypothesized that the ability of T.lucens to change its photosynthetic temperature optimum is associated with an adaptation to restrict water loss during summer drought. Campbell (1985) found a strong correlation between distribution

of restioids and "temperature ranges", suggesting that distribution of restioid species could be sensitive to this climatic factor. How the photosynthetic temperature optimum controlling ability of T.lucens fits in with the observed correlation between temeperature ranges and restioid distribution patterns cannot easily be explained. However, it can serve as a starting point in attempting to elucidate the links between fynbos plant form, plant function and population biology.

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APPENDIX

APPENDIX: The internal microcomputer of the data processor (DL-1) of the LCA-2 infra-red gas analyser (Analytical Development Company, Hoddesdon, England) was programmed to compute transpiration rate, stomatal conductance and net photosynthetic rate using the following equations:

1. e1 = saturated vapour pressure at cuvette air temperature

$$= 6{,}13753 \times \exp(ta(18{,}564 - ta/254{,}4)/(ta + 255{,}57)) \times 10^{-3}$$

(units : bars)

where ta represents cuvette air temperature

2. e2 = vapour pressure of water of air in cuvette

$$= e1 \times hc/100$$ (units : bars)

where h_c represents % relative humidity in cuvette

3. LH = latent heat of vaporization of water

$$= 2500 - (ta \times 2{,}36)18$$ (units : $J\ mol^{-1}$)

4. VF = Mass flow of dry air per unit leaf area

$= V \times 273/273+ta \times 1/22,4 \times 1/1,013 \times 10/A$ (units : $mol\ m^{-2}\ s^{-1}$)

where V represents flow rate of air supply unit in ml/s and

A " projected leaf area in cm^2

5. H = Radiation absorbed by the leaf

$= (PFD \times Ka)(0,8 \times 0.85 \times 0,2 \times 0,6)$ (units : $J\ m^{-2}\ s^{-1}$)

where

Ka = 698/3190 which converts $\mu Mol\ m^{-2}\ s^{-1}$ to $W\ m^{-2}$

0,8 = fraction of visible light absorbed by leaves

0,2 = fraction of infra-red light absorbed by leaves

0,85 = fraction of visible light transmitted through windows of leaf chamber

0,6 = fraction of infra-red light transmitted through windows of leaf chamber

PFD = photon flux density between 400 and 700 nm

therefore

$H = 0,175 \times PFD$

6. Δt = temperature difference between leaf and air

$$= H - LH(E)/ (0{,}93 \times Ma \times Cp/Rb + 4SB(ta = 273)^3)$$

where

E = transpiration rate (refer to equation 8)

Ma = 28,97 (molecular weight of air)

Cp = 1,012 $J\,g^{-1}\,K^{-1}$ (specific heat at constant temperature)

Rb = 0,144 $m^2\,s\,mol^{-1}$ boundary layer resistance specified for leaf chamber

SB = 5,7 x 10^{-8} $W\,m^{-2}\,K^{-4}$ (Stefan Boltzmann constant)

therefore

tl = leaf temperature

$= ta - \Delta t$

7. e3 = saturated vapour pressure at leaf temperature

$= 6{,}1078 \times e^{(17{,}27 \times tl/tl \times 237{,}3)}$ (units : bars)

8. Tr = transpiration rate

$= (e2/(P - e2)) \times VF$ (units : $m\,Mol\,m^{-2}\,s^{-1}$)

where

P represents barometric pressure

9. Rs = stomatal resistance to water vapour

$$= (e3/e2 - 1)/(VF - Rb) \qquad \text{(units : } m^2 s\, mol^{-1}\text{)}$$

and

$$Gs = 1/Rs \qquad \text{(units : } mol\, m^{-2} s^{-1}\text{)}$$

10. Cc = analysis reading of cuvette carbon dioxide concentration corrected for analyser cross-sensitivity to water vapour

$$= Co - EMAX(1 + 7{,}87 \times Co/1000) \times (1 - e^{(-0{,}07 \times e2 \times 1000)})$$

where

Co = analysis carbon dioxide concentration measured by LCA-2 analyser

EMAX = water vapour response of the LCA-2 analyser.

(An appropriate EMAX value was determined using methods as set out in the manual of the LCA-2)

11. Pn = net photosynthetic rate

$$= (Ci - Cc/P - e2) \times VF \qquad \text{(units : } \mu Mol\, m^{-2} s^{-1}\text{)}$$

where

Ci = reference carbon dioxide concentration measured by LCA-2 analyser

* Equation 4 was slightly modified to express VF for the ericoid species as mass flow of dry air per unit dry weight. Pn, Tr and Gs of the ericoid species were therefore expressed on a unit dry weight basis.

Pn = μMol g^{-1} min^{-1}

Tr = m Mol g^{-1} min^{-1}

Gs = m Mol g^{-1} min^{-1}

Transpiration rate and net photosynthetic rate of the restioid and broad-leaf species were expressed on a molecular weight basis using the following transformations:

transpiration rate (restiod and broad-leaf species)

1 mole H_2O = 18,01534 g

therefore 1 m Mol m^{-2} s^{-1} = 18,01534 mg x 1/100 dm^2 x 1/s

$\simeq$ 0,1801534 mg H_2O dm^{-2} s^{-1}

net photosynthetic rate (restioid and broad-leaf species)

1 mole CO_2 = 44,0103 g

therefore 1 uMol m^{-2} s^{-1} = 44,0103 mg/1000 x 1/100 dm^2 x 3600/h

$\simeq$ 1,58437 mg CO_2 dm^{-2} h^{-1}

TRANSPIRATION RATIO

for the ericoids:

TR = transpiration rate/net photosynthetic rate

= m Mol H2O/g min x g min/uMol CO2

= m Mol H2O/ m Mol CO2

but 1 mole H2O = 18,01534 g and

1 mole CO2 = 44,0103 g

therefore

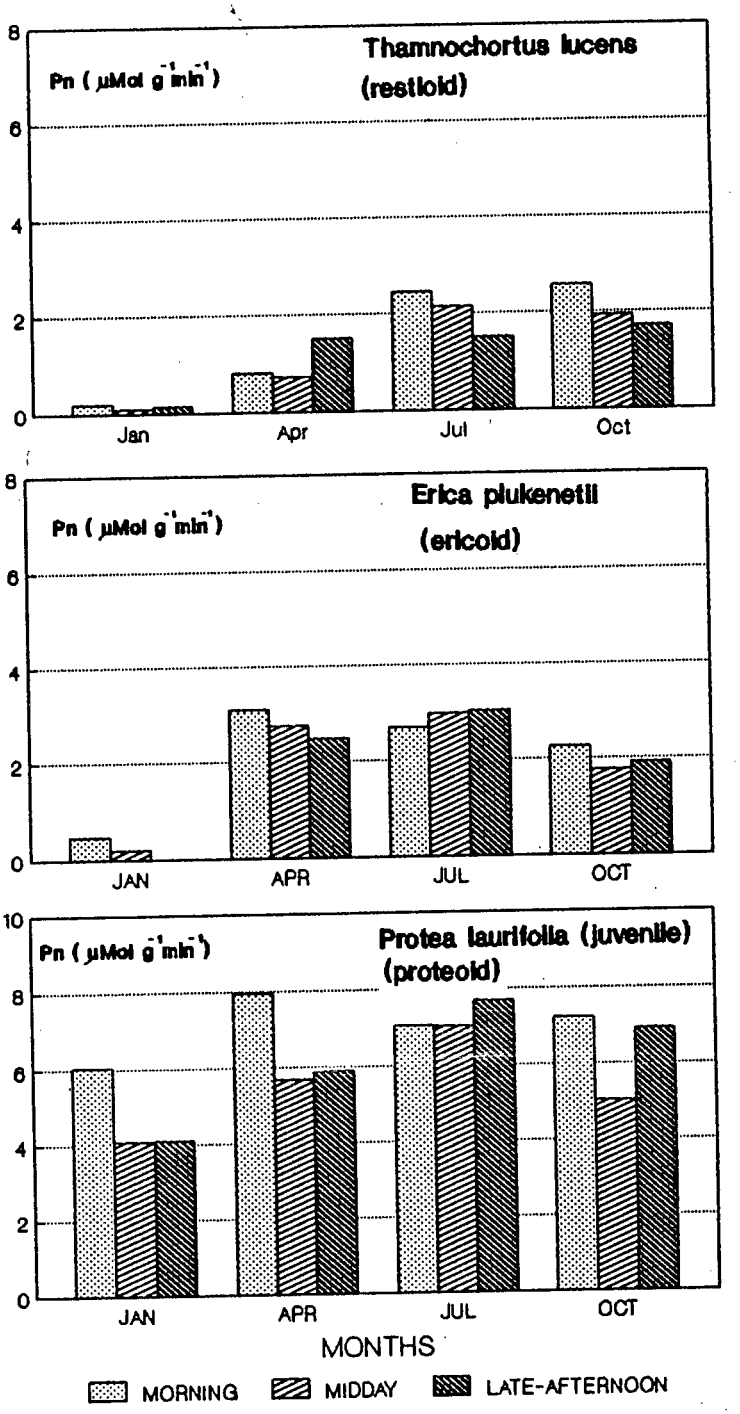
TR (ericoids) = Tr/Pn x 1000/1 x 18,01534/44,0103 (units : mgH2O/mgCO2)

for the restioids and the broad-leaf species:

TR = transpiration rate/net photosynthetic rate

= $mgH2O/dm^2 s \times dm^2 h/mgCO2 \times 3600$

= Tr/Pn x 3600 (units : mgH2O/mgCO2)



APPENDIX FIGURE 1: Diurnal variation in photosynthetic rate (µMol g^{-1} min^{-1}) of three representative mountain fynbos growth forms during January, April and July.

APPENDIX TABLE 1

Regression analysis was used to quantify the strength of the relationships between xylem pressure potential (xpp) and the following: stomatal conductance (Gs), net photosynthetic rate (Pn) and transpiration rate (Tr). The statistical procedures were performed for the linear (L), exponential (E) and multiplicative (M) regression models. The correlation coefficient (R) in addition to the variance probability level (P) for the strongest regression models are given in the table.

		Gs	Pn	Tr
Erica plukenetii	R	0.943 E	0.744 L	0.916 E
	P	0.0000	0.0549	0.0000
Erica hispidula	R	0.884 E	0.636 M	0.845 E
	P	0.0001	0.0263	0.0005
Thamnochortus lucens	R	0.831 E	0.627 E	0.806 E
	P	0.0008	0.0290	0.0016
Askidiosperma paniculatum	R	0.405 L	0.154 E	0.150 L
	P	0.1920	0.6335	0.6413

(continued on next page)

APPENDIX TABLE 1 (continued)

		Gs		Pn		Tr	
Protea laurifolia	R	0.678	E	0.604	M	0.136	M
(juvenile)	P	0.0154		0.0376		0.6730	
Protea laurifolia	R	0.753	L	0.476	E	0.059	E
(mature)	P	0.0047		0.1175		0.8562	
Leucadendron	R	0.551	E	0.443	L	0.364	L
salignum	P	0.0898		0.1488		0.2440	
Metrosideros	R	0.687	E	0.355	L	0.342	E
angustifolia	P	0.0136		0.2571		0.2768	

Appendix Table 2

Summarized data of cloudless days experienced at Hawequas weather station ($33^{o}44^{1}$ S : $10^{o}04^{1}$ E) from April 1983 to April 1986.

Number of Cloudless Days

Months	1983	1984	1985	1986	Average
January		27	19	24	23.33
February		26	21	20	22.33
March		22	17	22	20.33
April	16	19	12	19	16.5
May	16	16	15		15.67
June	15	17	15		15.67
July	20	19	13		17.33
August	18	18	14		16.67
September	20	19	15		18.0
October	22	17	16		18.33
November	20	24	18		20.67
December	24	20	20		21.33

Appendix Table 3

The average daylight for each month was determined from meteorological tables (List,1984) for the 35° southern latitude. Daylight was determined for 8 days (at 4 day intervals) and the average thereof (appearing below) was used for the calculation of average monthly carbon gain (AMCG).

Month	DAYLIGHT (hours)
January	14.2
February	13.35
March	12.28
April	11.23
May	10.27
June	9.85
July	10.02
August	10.83
September	11.87
October	12.87
November	13.93
December	14.47

APPENDIX TABLE 4

Diurnal variation in ambient air temperatures (^{o}C) at the three times during the day when photosynthetic gas exchange measurements were performed from January to December 1986.

	Morning	Midday	Late-afternoon
January	20	28	28
February	22	30	30
March	21	28	27
April	21	24	25
May	19,5	24	21
June	13	18	19
July	11	18	20
August	11	14	14,5
September	15	20	22
October	15	19	23
November	22	26	25
December	20,5	27	28